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FOSSIL LIZARDS FROM THE UPPER CRETACEOUS OF WESTERN CANADA

BY

GAO KEQIN ©

A THESIS
SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE
OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF ZOOLOGY

EDMONTON, ALBERTA

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ABSTRACT

Upper Cretaceous non-marine deposits of western Canada have yielded fossil lizards representing some 40 species in more than 30 genera and 10 families. Hundreds of specimens from geological formations of Aquilan, Judithian, and Lancian age (Campanian-Maestrichtian) reveal previously unknown aspects of the evolutionary history of several lizard families during the last 18 Myr of the Cretaceous Period in western Canada. On the basis of taxonomic composition and geological age, three assemblages are recognizable: 1) An Aquilan assemblage, known from the Milk River Formation, documents the earliest fossil record of the Iguanidae, Scincidae, Xenosauridae, Anguidae, and Necrosauridae, whereas the Teiidae are poorly recorded. 2) A Judithian assemblage, from the Oldman Formation, is composed predominantly of teiids; these are substantially different taxonomically from teiids of Lancian age and, hence, represent a distinct evolutionary stage of the family (this result is in contrary to that of previous authors, but is compatible with conclusions derived from mammalian evidence). This assemblage also includes the earliest helodermatids and varanids in North America. 3) A Lancian assemblage, from the Frenchman and Scollard formations, is generally the same as that of the type Lance Formation, Wyoming, but includes specimens of several new taxa, and others that allow taxonomic revisions of several species previously known from outside the study area.

Currently known fossil evidence suggests that the family Teiidae originated in the Early Cretaceous in North America, underwent an early diversification in both North America and Central Asia in the Late Cretaceous, but experienced a sharp decline at the end of the Cretaceous; the family may have invaded South and Central America before the Cretaceous-Tertiary transition. Once in South America the family underwent a Tertiary Neotropical radiation.

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The opportunity to undertake this research is based on significant field discoveries, and in this regard, all the field party members who worked under Dr. Fox's supervision since 1966 are acknowledged here. I thank Asta Voss, who sorted most of the specimens from screen washed concentrates, and Zhang Jingfen, who prepared some of the illustrations.

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LIST OF ABBREVIATIONS

A) Institutions:

AMNH: American Museum of Natural History, New York.

ANSP: Academy of Natural Sciences, Philadelphia, Pennsylvania.

CMN (=NMC): Canadian Museum of Nature (formerly National Museum of Canada), Ottawa, Ontario.

GSC: Geological Survey of Canada, Ottawa, Ontario.

MCZ: Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts.

MNA: Museum of Northern Arizona, Flagstaff, Arizona.

SMNH: Saskatchewan Museum of Natural History, Regina, Saskatchewan.

RTMP: Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta.

SMU: Southern Methodist University, Dallas, Texas.

UALP: Laboratory of Paleontology, University of Arizona, Tucson, Arizona.

UALVP (=UA): Laboratory for Vertebrate Paleontology, Departments of Geology and Zoology, University of Alberta, Edmonton, Alberta.

UCMP (=UC): Museum of Paleontology, University of California, Berkeley, California.

UMMZ: Museum of Zoology, University of Michigan, Ann Arbor, Michigan.

UNM: University of New Mexico, Albuquerque, New Mexico.

USNM (=NMNH): United States National Museum (= National Museum of Natural History, Smithsonian Institution), Washington, D. C..

YPM-PU: "Princeton Collection" now housed in Yale Peabody Museum (see Ostrom 1986 in Society of Vertebrate Paleontology News Bulletin).

YPM (=YUM): Peabody Museum, Yale University, New Haven, Connecticut.

ZPAL: Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

B) Localities:

AB: Altman Blowout (UCMP Loc. V-5616, Clemens 1963), Lance Formation, Lance Creek, Niobrara County, Wyoming.

BCA: Bug Creek Anthills (Sloan & Van Valen 1965; Estes et al. 1969), Hell Creek Formation, McCone County, eastern Montana.

BR: Blackbird Ridge, Judith River Formation, Golden Valley County, Montana.

BTB: Bushy Tailed Blowout (UCMP Loc. V-5711, Clemens 1963), Lance Formation, Lance Creek, Niobrara County, Wyoming.

DPP: Dinosaur Provincial Park (see, e.g., Dodson 1987; Eberth 1990b), Oldman Formation, Alberta.

GR: Gryde locality (Tokaryk & James 1989; Storer 1991), Frenchman Formation, in Sec. 19, Tp. 4, R. 18, W 3, Frenchman River Valley, southwestern Saskatchewan.

HC: Hell Creek Formation, McCone County, Montana (see BCA above).

IRV: Irvine locality (Fox 1968), Oldman Formation, in Sec. 31, Tp. 11, R. 2, W. 4, about 40 km east of Medicine Hat, southeastern Alberta.

KUA: The University of Kansas, Alberta locality (Clemens & Russell 1965; Lillegraven 1969), Scollard Formation, Red Deer River Valley near Scollard, central Alberta.

LC: Lance Creek Valley and environs (see Clemens 1963), various localities of the Lance Formation (including AB and BTB), Niobrara County, Wyoming.

MR: Laboratory for Vertebrate Paleontology, University of Alberta, Milk River locality (Fox 1972a), Milk River Formation, southern Alberta.

INTRODUCTION

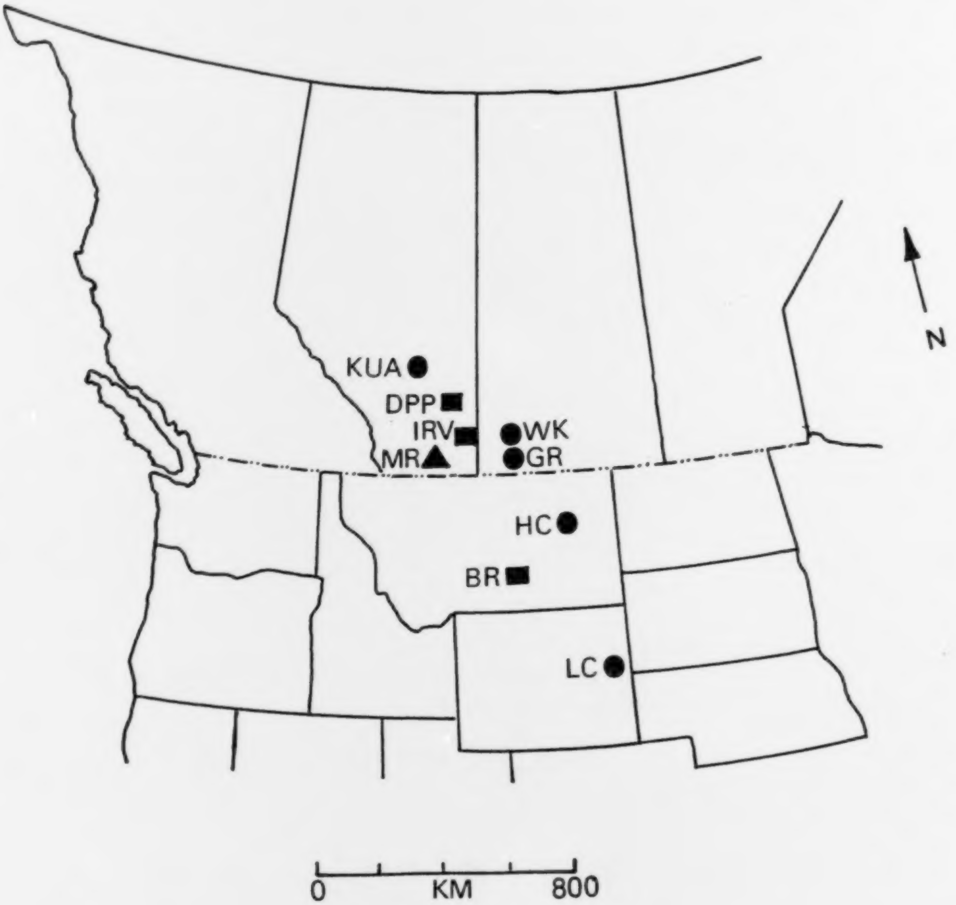
Lizards are the most successful modern reptiles in terms of their great specific and ecologic diversities, and wide geographical distribution. Osteologically, the group can only be diagnosed as primitive squamates lacking the specializations of amphisbaenians and snakes, but retaining such plesiomorphic character states as loss of the lower temporal bar and development of a highly mobile joint between the quadrate and squamosal, a condition commonly termed streptostyly. The true lizards in the sense of Estes (1983a-b) can be traced back to the Late Jurassic, but no lizards of this age can be referred to any modern lizard family, although infraordinal relationships with Recent groups can be determined. Early Cretaceous lizard fossils are poorly known, partly because of the worldwide transgression that submerged about one-third of the present land area of the Earth (Dott & Batten 1988; also see Funnell 1990). However, several recent discoveries have added significantly to the lizard fossil record of this age; these new discoveries include fossil materials from Central Asia (Nessov 1985, 1988; Alifanov 1989), Texas (Murry et al. 1989; Winkler et al. 1990), and undescribed material from Utah (R. L. Cifelli in litt. 1991). Study of Late Cretaceous lizard fossils is especially significant, since the Late Cretaceous appears to have been an important period for the establishment and early diversification of most modern lizard families (Estes 1983b); furthermore, the widely exposed fossiliferous non-marine deposits in the Western Interior of North America and use of highly productive screen-washing techniques for recovery of small vertebrate fossils (J. B. Hatcher 1896; McKenna 1960; Clemens 1963; Lillegraven 1969) have provided a unique advantage in undertaking this study.

In North America, the first discovery of fossil lizards from the Upper Cretaceous was associated with paleontological exploration during the period 1889-1892 in Converse County (now Niobrara County), Wyoming. Marsh (1892) made the first report of Late Cretaceous terrestrial lizard fossils naming Chamops segnis (based on an incomplete dentary) and Iguanavus teres (based on several vertebrae) from the "Laramie Formation" of Wyoming (the "Laramie Formation" was later renamed [Stanton 1910] as the Lance Formation). Work since has shown that Chamops segnis is a common Late Cretaceous lizard and Iguanavus teres is possibly the synonym of the former (Estes 1964, 1983a), or a nomen dubium as treated in this paper. During this period of time, although several thousand isolated teeth, jaws, and other materials of a variety of vertebrates had been found by J. B. Hatcher (chief collector for O. C. Marsh) and his assistants (based on these materials for example, Marsh named 18 new genera and 32 species of mammals), no special attention was paid to lizards except for the two forms mentioned above (Gilmore 1928).

Gilmore (1928) made the pioneer contribution to the systematic study of Late Cretaceous lizards from North America. In his monograph "Fossil Lizards of North America", Gilmore described 17 species in 12 genera from the Lance Formation of Wyoming and equivalent beds elsewhere; among these, 13 species in 10 genera were new, and seven species in seven genera are still valid today, with the others having been emended since (Estes 1964, 1983a). Few subsequent papers in this field were published, until Estes' (1964) comprehensive work on small non-mammalian vertebrates from the Lance Formation, eastern Wyoming. Other North American Late Cretaceous lizards were reported by Estes et al. (1969) from the Hell Creek Formation, Montana; by Sahni (1972) from the Judith River Formation, Montana; by Armstrong-Ziegler (1978, 1980) and Sullivan (1981) from the Fruitland Formation, New Mexico; and more recently by Parris & Grandstaff (1989) and Denton et al. (1991) from New Jersey. Estes (1983a) provided the first and the most recent taxonomic codification of the data on all fossil lizards known at the time: his "Sauria Terestria, Amphisbaenia" contribution to the "Handbuch der Palaoherpetologie" included 18 species in 17 genera of Late Cretaceous lizards from North America.

In western Canada, early discoveries of Late Cretaceous terrestrial lizards were coincident with a period called the "Great Canadian Dinosaur Rush," from 1912 to 1925 (see Koster et al. 1987). Gilmore (1923) marked the first report of Late Cretaceous lizard from western Canada by referring a nearly complete dorsal vertebra (UA 112) to "a lacertian" (= lacertilian). The specimen was found by G. F. Sternberg in 1921, at Sandy Point, South Saskatchewan River, near Empress, southeastern Alberta (Belly River Formation, now Oldman Formation, Russell & Landes 1940). Later reports of Cretaceous lizards from western Canada were given in descriptive papers by C. M. Sternberg (1951), Waldman (1970); and in faunal lists by L. S. Russell (1935, 1964), Russell & Landes (1940), Fox (1972a, 1976, 1989), Currie (1986), Eberth (1987), and Koster et al. (1987).

This study focuses on fossil lizards from geologic formations of Aquilan, Judithian, and Lancian age in western Canada, covering a geologic span of approximately 18 Myr (Lillegraven & McKenna 1986; Harland et al. 1990). As mentioned above, previous work was mainly on the fossils of Lancian age, while pre-Lancian lizards were poorly known in North America compared to dinosaurs, mammals, and other vertebrates of the same age. The major concern of this study is the fossil lizards from the Oldman and Milk River formations. The former formation is about 11 Myr and the latter 18 Myr earlier than the Lance and Hell Creek formations (Lillegraven & McKenna 1986; Harland et al. 1990). The newly discovered lizards from the Oldman Formation indicate that the Judithian lizard fauna is substantially different from that of Lancian age, contrary to the conclusion from previous authors (see Sahni 1972; Armstrong-Ziegler 1978, 1980; Sullivan 1981; Estes 1983a). This study shows that most lizard specimens from the Oldman Formation are representives of new genera and new species. Some are referrable to genera occurring in Lancian horizons, but none can be definitely assigned to Lancian species. This result is consistent with the mammalian evidence that shows less than five percent of mammalian species of Judithian age are the same as those of Lancian (see Lillegraven & McKenna 1986). The Milk River lizards document an early diversification of several modern families, especially Scincidae, and include the earliest fossil record of iguanids from anywhere in the world. These newly discovered lizards represent important components of the North American Late Cretaceous non-mammalian vertebrate fauna, and a general comparison of these lizards with those of the same age from the Eurasian continent gives a more complete picture and a better understanding of the evolutionary history, paleobiogeography, and paleoecology of the relevant modern lizard families.



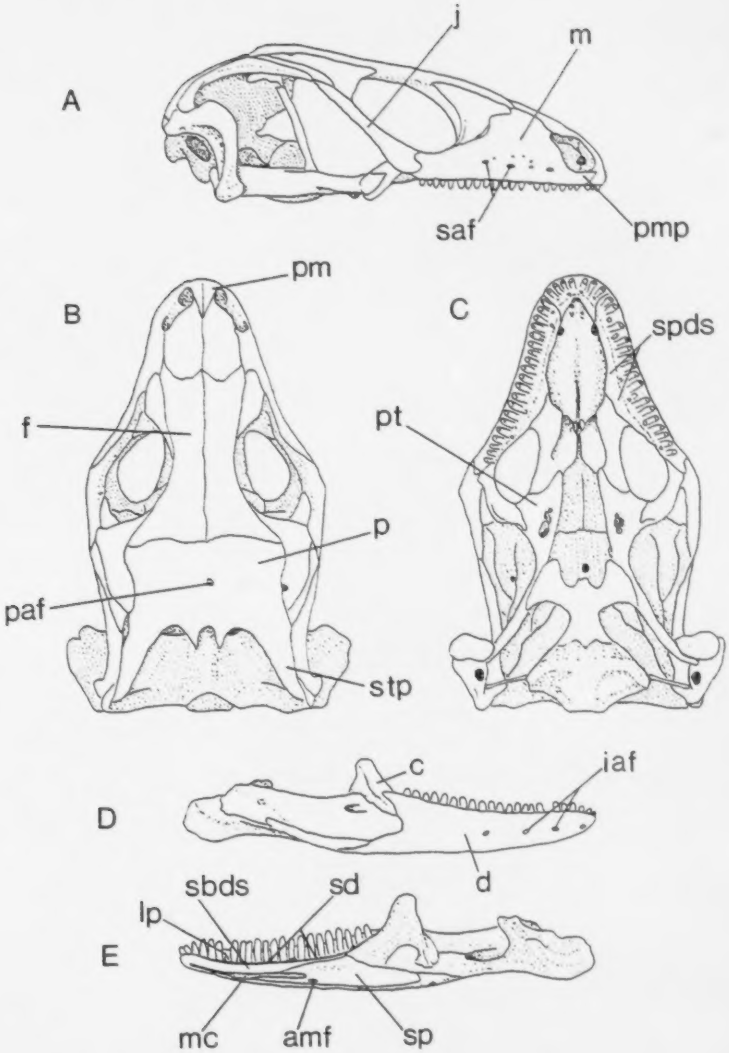
Text-fig. 1. Geographical distribution of the Upper Cretaceous lizard localities in western Canada and nearby area (Montana and Wyoming). Solid triangle indicates Aquilan locality in the Milk River Formation, Alberta; solid rectangles indicate Judithian localities of the Oldman and Judith River formations, Alberta and Montana; solid dots indicate Lancian localities of the Scollard (Alberta), Frenchman (Saskatchewan), Hell Creek (Montana), and Lance (Wyoming) formations. Abbreviations as listed in p. xvii.

MATERIALS AND METHODS

This study is mainly based on fossils collected from the Upper Cretaceous Milk River, Oldman, Frenchman and Scollard formations, western Canada; but some specimens from the Lance and Hell Creek formations, in the United States, are also included because they provide new information for a better understanding of the relevant taxa, and provide materials for recognition of new taxa that have close relatives in the study area. The specimens from the Milk River Formation were collected by UALVP field parties from 1968 to 1970. The Oldman specimens are in the collections of both UALVP and RTMP, from several localites in southern Alberta, made from 1966 to the present. The specimens from the Frenchman Formation were collected by the SMNH and UALVP parties from 1979 to 1984. All the new materials from the Lance and Hell Creek formations used in this study are in the UALVP collections, obtained from field work in 1969-1976. Finally, the UALVP Scollard lizards were recently sorted from screened concentrate originally collected during 1964-1967 by University of Kansas field parties (Lillegraven 1969).

The specimens used in this study are mostly tooth-bearing maxillaries and dentaries. These provide materials for the recognition of a number of new taxa of lizards, as well as assistance in understanding the phylogenetic relationships of several previously known species. Other materials in the available collections include disarticulated skull elements, such as frontals, parietals, jugals, pterygoids, premaxillaries (see Text-fig. 2 for anatomical positions), and disarticulated vertebrae and limb bones. These latter elements in most cases are unreliable for identification at generic and specific levels without reference to articulated skulls or skeletons; however, in certain groups, such as the Xenosauridae, the disarticulated skull elements show a characteristic sculpture pattern for certain species. The identification of jaw material is mainly based on dental morphology (tooth form and cusp pattern) and general jaw configuration. Tooth form and cusp pattern are also important for ecological interpretations, as the connections between dental morphology and food preference of lizards have been shown in several papers (Lonnberg 1903; K. P. Schmidt 1919; Cowles 1930; Hotton 1955; Presch 1974b; Greene 1982; Estes & Williams 1984). These studies have demonstrated that the tooth type and the particular cusp pattern as well as the pattern of wear provide indirect evidence as to the possible habit and diet of the animal (Presch 1974b: 344): "tooth structure and form appear to be strongly influenced by selective factors operating through the food supply and diet demands of the animal".

Most of the specimens for this study have been obtained through screen washing in the field, with some relatively large specimens collected by surface picking from outcrops. When necessary, specimens were prepared under a Wild M-7 microscope in the laboratory. All holotype and well-preserved specimens are figured in the photoplates, and they are mostly illustrated in the text-figures. The photographs were taken by using an Olympus OM-2s camera with 50 mm macrolens with bellows. The text-figures were drawn with assistance of a camera lucida. All measurements of the specimens are in millimeters.



Text-fig. 2. Skull and mandible of Eumeces obsoletus (Scincidae), showing anatomical structures of lizards (from Estes et al. 1988). Skull in lateral (A), dorsal (B), and ventral (C) views; mandible in lateral (D), and medial (E) views. Abbreviations for this and all following Text-figures: aif, anterior inferior alveolar foramen; amf, anterior mylohyoid foramen; c, coronoid; d, dentary; f, frontal; iaf, inferior alveolar foramen; ims, intramandibular septum; j, jugal; lp, lateral parapet of dentary; m, maxillary; mc, meckelian canal; p, parietal; paf, parietal foramen; pm, premaxillary; pmp, premaxillary process; pt, pterygoid; saf, superior alveolar foramen; sbds, subdental shelf; sp, splenial; spds, supradental shelf; stp, supratemporal process of parietal; sd, sulcus dentalis.

GEOLOGICAL SETTING

The fossil specimens used in this study were collected from three horizons, chronologically from old to young: the upper member of the Milk River Formation (Dowling 1917; Russell & Landes 1940), early Campanian (Williams & Burke 1964; Fox 1976; Lillegraven 1991) or Aquilan (NALMA, L. S. Russell 1964; Lillegraven & McKenna 1986) in age; the Oldman Formation (Russell & Landes 1940), mid-Campanian (L. S. Russell 1975; Eberth 1987) or Judithian (NALMA, L. S. Russell 1964; Lillegraven & McKenna 1986) in age; and the Frenchman Formation (Furnival 1946) and its equivalent Scollard (Irish 1970; Gibson 1977; Lerbekmo & Coulter 1985), Lance (Stanton 1910) and Hell Creek (Brown 1907) formations, all late Maestrichtian or Lancian (Dorf 1942; L. S. Russell 1964; Lillegraven & McKenna 1986) in age. These formations accumulated on the coastal plain adjacent to the Western Interior Seaway during Campanian-Maestrichtian time. The main source of these sediments was from the then-uplifting Rocky Mountains (Price & Mountjoy 1970; Rahmani & Lerbekmo 1975; Eberth 1990a) west of the seaway.

I. Paleogeography and Depositional History

At the time when the upper member of the Milk River Formation was deposited (early Campanian), the North American continent was divided by the Western Interior Seaway, which extended from north to south along the eastern side of the Rocky Mountains and linked the Arctic Ocean with the Gulf of Mexico (see, e.g., Williams & Stelck 1975; Funnell 1990; Nicholls & Russell 1990). The shallow epeiric sea covered most of what is now Alberta, southeastern Saskatchewan, eastern Montana, Wyoming, Colorado, northeastern New Mexico and Texas. In western Canada, continental deposits of that age were only exposed in southern Alberta.

By mid-Campanian time, the rising Rocky Mountains caused the retreat of the Interior Sea to the east and the deposition of detritus in the Mackenzie River valley of the Northwest Territories, in Alberta and western Saskatchewan, and in Montana, Wyoming, and New Mexico (Williams & Stelck 1975, text-fig. 7; Funnell 1990, fig. 11). The Oldman Formation and the upper part of the Judith River Formation, Montana, were formed about the same time. Lizard fossil-bearing non-marine deposits of the same age are also known from New Jersey, one of the few occurrences of non-marine vertebrates on the eastern side of the Late Cretaceous epeiric seaway (Parris & Grandstaff 1989; Denton et al. 1991).

By late Campanian-early Maestrichtian time, the last major transgression of the Interior Sea (Bearpaw Sea, see Caldwell et al. 1978) covered a large area including Alberta north of the Peace River Arch (Wall 1973, 1975) and west to the edge of the foothills in southern Alberta and Montana (Williams & Stelck 1975). Continental deposits developed in central and western Alberta, and in central Saskatchewan (Edmonton Group and St. Mary Formation); however, lizard fossils are rarely recovered from these deposits, except for a Chamops-like teiid from the Wapiti Formation, northwestern Alberta (see later discussion). In northwestern New Mexico and southwestern Colorado, the Fruitland Formation was probably deposited at about this time: the age of the formation has been determined as Judithian on pollen (Fassett & Hinds 1971), ammonites and radiometric dating (Cobban 1973; Fassett 1987; Brookins & Rigby 1987), and vertebrate faunal comparison with Lancian and Judithian assemblages from Wyoming and Montana (L. S. Russell 1975; Fox 1978; Armstrong-Ziegler 1980; Lillegraven & McKenna 1986; Lucas et al. 1987; Rigby & Wolberg 1987); but more recently as Edmontonian, not Judithian, based on mammalian fossils (Lillegraven & Ostresh 1990).

In the latest Cretaceous, over-filling of sediments from the west accompanying uplift in the Mackenzie Mountains region caused the regression of the late Maestrichtian Sea from the Western Interior (Williams & Stelk 1975). At the same time, extensive clastic deposits were developed in Alberta (Scollard Formation), Saskatchewan (Frenchman Formation), Wyoming (Lance Formation), and Montana (Hell Creek Formation). A rich fossil vertebrate fauna, including a large number of lizard taxa, has been found in these deposits.

II. Geological Formations

Within the study area, Upper Cretaceous non-marine deposits are mainly composed of sandstones, siltstones, and shales, and are extensively exposed along the river valleys and occasionally, in badlands. Various authors have given detailed descriptions of these deposits; here briefly, the lizard fossil-bearing non-marine sediments include the following formations:

Milk River Formation

The Milk River Formation is approximately equivalent to the Eagle Formation of Montana. The formation is exposed along the Milk River and its tributaries in southern Alberta. Having a maximum thickness of about 77 m (Russell & Landes 1940), the Milk River Formation can be subdivided into upper and lower members. The lower member (maximum thickness of 41 m) is dominantly marine in origin, characterized by dark shales grading upward into medium-grained sandstones with concretions. The upper member is composed of non-marine, drab grey, brown and dark grey argillaceous sandstones and sandy shale with streaks of impure lignite (Russell & Landes 1940; Crockford & Clow 1965). The upper member is about 36 m in maximum thickness (Russell & Landes 1940), and is Aquilan (early Campanian) in age (L. S. Russell 1964; Fox 1976; Lillegraven 1991).

L. S. Russell (1935) recorded the discovery of fossil molluscs and vertebrates from the upper member of the Milk River Formation, from which a fragmentary dentary (GSC 8721) was listed as Lacertilia incertae sedis. Recently, Fox (1968, 1969, 1970, 1971, 1972a-b, 1984, 1985) reported a series of important discoveries of mammalian fossils from the upper member of the formation exposed in Verdigris Coulee, including the geologically youngest triconodonts and symmetrodonts, primitive lipotyphlan insectivores, and diverse early marsupials. Fox (1972a) also published a faunal list, which included six lizard taxa associated with those of elasmobranchs, actinopterygian fishes, salamanders, turtles, champsosaurs, crocodiles, dinosaurs, and mammals. The lizards are described here for the first time.

Oldman Formation

The Oldman Formation is composed of non-marine deposits in Alberta that correlate with the upper part of the Judith River Formation of Montana (L. S. Russell 1964; Eberth 1987; Thomas et al. 1990). The name "Oldman Formation" was proposed by Russell & Landes (1940) as the substitute of commonly called "Pale beds" and the upper division of Dawson's (1881) Belly River Series. McLean (1971, 1977) recommended to drop the "Oldman" from the nomenclature of east-central Alberta and extend the use of "Judith River" into this area. His motion has been followed by some authors but rejected by others (e.g., Rahmani & Lerbekmo 1975; Fox 1976, 1978). In the current relevant literature, both "Oldman" and "upper Judith River" are used for the same geologic formation in southern Alberta. The name "Oldman Formation" remains in this paper as Russell & Landes (1940) defined it, for its convenient use as a geographically extensive, lithological mappable unit (J. F. Lerbekmo, pers. comm.). The characteristic rocks of this formation are pale grey bentonitic sandstones, with interbeded grey and brown shales (L. S. Russell 1964). Coal seams are only seen at the top of the formation (ibid.). The outcrops of the formation are widely exposed in southern Alberta (along the Milk River, and the South Saskatchewan River, north of Medicine Hat), and are best exposed in the Dinosaur Provincial Park, along the Red Deer River north of Brooks. The thickness of the formation as known from drilling is about 127 m in the Irvine area, increasing southward to about 180 m in the Manyberries area (Crockford & Clow 1965). The formation has yielded radiometric dates of about 76 Myr (Thomas et al. 1990), and a large vertebrate fauna (summarized in L. S. Russell 1964; Langston 1965; Fox 1976; Currie 1986; Eberth 1987; and Koster et al. 1987). The faunal lists given by Currie (1986), Eberth (1987), and Koster et al. (1987) included as many as 11 lizard taxa (but see later discussion). Within the uppermost 100 m of the formation, a recently recognized disconformity reflects a major Campanian uplift event in the Cordillera (Eberth 1990a-b), and recent studies of the 24 microfossil localities above and below the disconformity (Dodson 1983, 1987; Brinkman 1990; Eberth 1990b) have yielded important results relevant to the sedimentology and the paleoecology of the formation.

Gilmore (1932) named *Polyodontosaurus grandis*, a supposed lizard, on the basis of a small dentary (NMC 8540) from the Belly River Formation (= Oldman and Foremost formations, see Lerbekmo 1989). But later work by C. M. Sternberg (1951) and D. A. Russell (1969) indicated that the specimen actually belongs to a carnivorous dinosaur (Troodontidae); D. A. Russell (1969) regarded *Polyodontosaurus grandis* as a synonym of *Stenonychosaurus inequalis*, which is now commonly agreed to be a synonym of *Troodon formosus* Leidy 1856 (Currie 1987; D. A. Russell 1989; Osmolska & Barsbold 1990).

The Wapiti Formation (Dawson 1881) in northwestern Alberta may include nonmarine deposits that are younger than Oldman Formation (Allan & Carr 1946; Langston 1965). C. M. Sternberg (1951) described a lizard (*Chamops* cf. [*C.*] *segnis*) from member B of the Wapiti Formation, Kleskun Hills near Grande Prairie. The age of the formation ranges from Campanian to Maestrichtian (Stott 1975), whereas member B of the formation is probably late Campanian or somewhat younger in age. Recent discovery of the ceratopsian Pachyrhinosaurus in the same formation at Pipestone Creek by RTMP field parties may indicate that at least part of the formation is equivalent to the Horseshoe Canyon Formation of central Alberta, and hence is Edmontonian in age (Tanke 1988; Dodson & Currie 1990).

Lance Formation and Equivalents

The Lance Formation of eastern Wyoming and its equivalent Hell Creek Formation of eastern Montana are somewhat outside the region for this study, and the lizard fossils from these formations have been previously described by Marsh (1892), Gilmore (1928), Estes (1964, 1969b, 1983a), and Estes et al. (1969). However, new specimens collected by UALVP field parties during the 1969-1976 period yield new information requiring a review of certain known taxa, and more importantly provide the specimens for recognition of several new lizard taxa, which are closely related to those in the study area; therefore, these specimens are also included in this paper.

Exposed mostly in the Powder River Basin of eastern Wyoming, the Lance Formation consists of a succession of interbedded siltstones, channel sandstones, shales, and lignites (Clemens 1960, 1963; Estes 1964). The earliest discovery of vertebrate fossils from this formation was reported by Marsh (1889), who referred to the deposits as to the "Ceratops beds." Since then, a series of names have been used for the deposits ("Lance Creek beds," "Converse County beds," "Laramie beds," and "Lower Fort Union:" see Clemens 1963, Estes 1964 for earlier citations) until Stanton (1910), who named the unit as the Lance Formation. The formation is overlain by the Fort Union Formation and underlain by the brackish water sediments of the Fox Hills Formation. The maximum thickness of the formation is about 750 m in the type area (Clemens 1963). The lizard fossils previously reported from this formation represent about 13 species in 13 genera (Estes et al. 1969; Estes 1983a).

The Hell Creek Formation consists of non-marine deposits overlying the Fox Hills Formation (brackish water deposits) in eastern Montana. The formation is mainly composed of grey to brown sandstones and shales (L. S. Russell 1964) of fluvial origin (Fastovsky 1987). The maximum thickness of the formation is about 100 m along Hell Creek (Brown 1907), but varies in adjacent areas (see Archibald 1982). The Bug Creek Anthills (BCA) and nearby localities in the Hell Creek Formation have yielded an important vertebrate fauna (Sloan & Van Valen 1965; Estes et al. 1969; Estes & Berberian 1970), which has figured importantly in recent debates concerning the events at K-T boundary in North America and the timing of aspects of mammalian evolution. As Archibald (1982) pointed out, the major argument centres on the age of the fauna -- whether the BCA fauna is younger than or essentially comtemporary with the Lancian fauna. Estes et al. (1969) and Estes & Berberian (1970) stressed the overall similarities in the components of the two faunas, suggesting the "time of deposition of the upper parts of both the Lance Formation and the Hell Creek Formation was essentially synchronous" (Estes & Berberian 1970: 9); whereas Archibald (1987a-b) and Sloan (1987) proposed a Bugcreekian Age (Stage) in recognizing the age of the BCA local fauna as younger than Lancian. Since the evidence is not decisive, the latter proposal has not been widely accepted, although the uppermost parts of the Hell Creek Formation include Paleocene deposits (Archibald 1982).

In central Alberta, Lancian rocks are represented by the Scollard Formation, formerly called "the upper part of the Edmonton Formation," "the Upper Edmonton Formation" (see Lillegraven 1969), or "the Scollard Member" of the Paskapoo Formation (Irish 1970). The Scollard Formation, as Gibson (1977) defined it, includes Paleocene deposits at its top. Lithologically, the formation "consists of an interbedded, interfingering sequence of argillaceous sandstone, siltstone, mudstone, and shale. Minor amounts of coal (Seams Nos. 13, 14), bentonite, and tuff occur in the formation" (Gibson 1977: 7). The maximum thickness of the formation is about 85 m in the Huxley-Big Valley area (ibid.), and coal seam 14 (Paleocene part, about 18 m above the K/T boundary) has recently yielded a radiometric date of 63 Myr (Lerbekmo & Coulter 1985). The Scollard Formation unconformably rests on the Battle Formation, which contains a layer of volcanic deposition called the Kneehills Tuff, dated as 65-66 Myr (Folinsbee et al. 1965; also see Lerbekmo & Coulter 1985). Fossil lizards were previously unreported from the Scollard Formation, although a rich mammalian fauna from several localities along the Red Deer River Valley has been reported and described (see Clemens & Russell 1965; Lillegraven 1969).

In southwestern Saskatchewan, the northward extension of the Hell Creek Formation of eastern Montana is called the Frenchman Formation, which was previously known as the "lower Ravenscrag" (see Russell & Landes 1940; Furnival 1946; Johnston & Fox 1984). The formation is mainly composed of coarse grained greenish-brown sandstones, silty sandstones, and shales (Furnival 1946), and rests on the Whitemud and Battle formations at an unconformable contact. The maximum thickness of the formation is about 100 m (L. S. Russell 1964), representing the terrestrial sediments of the last 1.5 Myr of Late Cretaceous time (Lerbekmo 1987).

The earliest discovery of lizards from the Frenchman Formation was in 1921 by C. M. Sternberg (see Gilmore 1928: 18; GSC 2912, a caudal vertebra, originally cited as from the Lance Formation, Rocky Creek, Saskatchewan). Later reports of vertebrate fossils from the formation were made by L. S. Russell (1964), Fox (1989), Tokaryk & James (1989), and Storer (1991).

DENTAL MORPHOLOGY AND TERMINOLOGY

In this section, I define dental terms used subsequently and explain their use as appropriate, pointing out some of the ambiguities and even errors in previous work on lizard anatomy and systematics, including the use of mammalian nomenclature for the dental anatomy of lizards.

Tooth Form

It is common in lizards that the primitive reptilian homodont dentition has been modified by a differentiation of the marginal teeth, resulting in some degree of heterodonty. The anterior teeth of some lizards are enlarged and canine-like (caniniform), the lateral or cheek teeth may be conical, bicuspid, tricuspid, multicuspid, crested, or even enlarged to form crushing plates. Estes & Williams (1984) have recently compiled the data on the development of heterodonty in various groups of lizards.

The evolution of heterodonty in lizards is largely associated with the variety of feeding habits and different dietary demands. For example, the combination of sharp anterior conical teeth with bicuspid or tricuspid cheek teeth seems best adapted for capturing and eating insects with chitinous exoskeletons (Hotton 1955); while blunt anterior conical teeth combined with greatly expanded posterior crushing teeth seems designed for feeding on hard-shelled beetles or even molluscs (Conant 1955).

Except for the acrodont dentition of adults in some groups (agamids, chamaeleons, amphisbaenians), the marginal teeth of most lizards are replaced a number of times during their life history (see, e.g., Edmund 1969). Thus, the teeth of most lizards are polyphyodont. However, some teiids show replacement suppression as adults (see MacLean 1974).

Tooth Implantation

It is generally considered that there are basically three types of tooth attachment in reptiles, namely, **acrodont**, in which the tooth is ankylosed to the summit of the jaw (also see discussion in Gauthier et al. 1988; Estes et al. 1988); **pleurodont**, in which the tooth is attached to the inner surface of the lateral wall of the jaw (most lizards); and **thecodont**, in which the tooth root is sheathed in a deep socket in the jaw (mosasaurs). However, as Romer (1956) has pointed out, the distinctions between these classic types have tended to break down owing to increasing knowledge of fossil and living reptiles. Besides the three terms above, at least the following have been used in the literature to describe intergrades between the basic types of tooth implantation: **protothecodont**, **subthecodont** (Camp 1923; Edmund 1969); **subacrodont** (Estes 1964), **hyperacrodont** (Camp 1923; Malan 1963), **pseudoacrodont** (Sulimski 1978); **subpleurodont** (Estes 1964), **pleurothecodont** (Gilmore 1928); **ankylothecodont** (Chatterjee 1974; Benton 1983). These terms have certainly enriched our vocabularies in the recognition of intermediate conditions between the three classic types of tooth attachment, but they also cause confusion.

Using different terms for the same condition of tooth attachment results in ambiguities, since the differences between "protothecodont" and "subthecodont", "subpleurodont" and "pleurothecodont", and "subacrodont, "pseudoacrodont", and "hyperacrodont" are not obvious. I prefer to use the first term in each pair or group above as supplementary terms for the intergrades between the three classic types of tooth implantation.

Specifically, protothecodont is appropriate for the condition in some early reptiles, such as cotylosaurs and pelycosaurs; subpleurodont (sensu Estes 1964) for the condition between pleurodont and subacrodont, as is commonly seen in teiids; and for those aberrant teiids, such as Haptosphenus (Estes 1964) and Adamisaurus (Sulimski 1978). The term ankylothecodont has been clearly defined for the specialized tooth implantation seen in rhynchosaurs, in which the marginal teeth are fused in the sockets as a combination of acrodonty and thecodonty. This type of tooth attachment is unknown in any lizards. Vorobyeva & Chugunova (1986) use "hyperpleurodontal attachment" in respect to the dentition of gekkos, a condition termed as pleurodont by most other authors.

Using the same term for different modes of tooth attachment also engenders confusion. For example, Camp (1923) used the term "hyperacrodont" for the pattern in Sphenodon, Agamidae, and Chamaeleonidae (a mode of implantation now commonly termed acrodont), while Malan (1963) used the same term "hyperacrodont" to describe the condition seen in Howesia, a South African rhynchosaur, which is more appropriately termed ankylothecodont (Chatterjee 1974; Benton 1983). Another example is that of Camp (1923), who used the term "subthecodont" for Chamops (more appropriately termed subpleurodont by Estes in 1964), while the term "subthecodont" has been more recently used as substitute for "protothecodont" in most early reptiles (see Edmund 1969).

Terms Used in Text

In this study, technical terms for osteological and dental features of lizards are mostly adopted from previous authors, including Goodrich (1930), Estes (1964, 1983a), Romer (1956), Edmund (1969), Estes et al. (1988). Since some terms are not commonly used in the description of fossil reptiles other than lizards, it is necessary to define them explicitly as follows:

Inferior alveolar foramina: mental foramina in the lower jaw through which passes the inferior alveolar branch of Cranial Nerve V_3 (Estes 1964; Northcutt 1979).

Interior alveolar canal: a canal for the blood vessels and nerves supplying the teeth and lateral surface of the jaws; includes the superior alveolar canal in the maxillary and the inferior alveolar canal in the dentary (Estes 1964; Northcutt 1979).

Interior alveolar foramen: internal opening of the superior or inferior alveolar canal within the upper or lower jaws, including an anterior interior alveolar foramen and a posterior interior alveolar foramen (see Estes 1964).

Internal Meckelian foramina: internal mandibular foramina (Goodrich 1930), including anterior Meckelian foramen, anterior alveolar foramen, anterior mylohyoid foramen, and the posterior mandibular foramen (fossa) in the lower jaw, for the passage of mandibular nerve branches and blood vessels supplying the mouth floor and the tongue (Romer 1956).

Intramandibular septum: a partition posteriorly located within the Meckelian canal, functioning in separating Meckel's cartilage from the lateral nerves and blood vessels (Estes 1964; Estes et al. 1988).

Subacrodont: attachment of the marginal teeth mostly to the jaw summit, but also to the remaining lateral parapet, which is one-third or less of the tooth height (see Gao & Fox 1991); this condition is usually associated with loss of the sulcus dentalis.

Subdental shelf: a shelf-like medial extension of the dentary below the tooth row (Estes et al. 1988), often contributing to the sulcus dentalis and the dorsal splenodentary articulation in the lower jaw.

Subpleurodont: attachment of the marginal teeth to the medial surface of the lateral parapet of the jaw, which remains low as less than one-half to one-third of tooth height (Estes 1964; Gao & Fox 1991).

Superior alveolar foramina (= maxillary foramina, Du Bois 1943): superior labial foramina (Estes 1964) on the maxillary, through which passes the superior alveolar branch of Cranial Nerve V_2.

Supradental shelf: a shelf-like medial extension of the maxillary above the tooth row, often bearing an anterior vomerine process and a posterior palatine process (Estes 1964).

Sulcus dentalis: dental gutter separating the tooth bases from the supradental ridge of the maxillary and from the subdental ridge of the dentary (Estes 1964).

Terms Unsuitable for Dental Description in Lizards

Certain terms have been inappropriately used in the literature on the dental morphology of lizards. The relevant publications are scattered; the terms listed below are only those that I have encountered in an incomplete survey of the literature.

"Triconodont" and **"symmetrodont"**: Some authors (Camp 1923; Gilmore 1928; Twente 1952; Savage 1963; Presch 1970, 1974a-b; Estes 1983a; Estes & Williams 1984; Winkler et al. 1990) apply terms "triconodont", "trilobate"(Camp 1923), "tritubercular", or "symmetrodont" referring to lizard teeth having three cusps.

Contrary to Estes & Williams (1984), who favor the term "triconodont", I strongly suggest using "tricuspid" to replace this and other terms applied to teeth having three cusps. "Triconodont", "symmetrodont" and "tritubercular" are terms that have been conventionally used as the basis for taxonomic names for certain groups of fossil mammals or as descriptive terms for mammalian dentitions, so that use of these terms for lizards is inappropriate and can only render confusion. "Trilobate" is so close in spelling to Trilobites (the synonym of Janassa, a chondrichthyan fish, see Romer 1966: 351) and "trilobites" (a group of arthropod invertebrates) that use of these terms for lizards should be avoided, in order to designate clearly the dentition of lizards. Similarly, "bicuspid" is considered to be a better term than "biconodont" for those tooth crowns having two cusps.

"Molar" and **"molar hypertrophy"**: "Molars" are the unreplaced postcanine teeth of mammals (Romer 1966: 191); therefore, this term is best restricted to mammals, and should not used for other vertebrates, even for the ancestral stock of mammals (mammal-like reptiles). Smith (1946: 7) stated that "in the Agamidae the tooth modification is carried still further, to such a point that molars, incisors, and canines may be distinguished; the parallelism with the mammalian condition is emphasized by the fact that the molars are not replaceable whereas the other teeth are". In fact, this statement is incorrect. Some agamids indeed develop anterior enlarged, canine-like teeth (but not the canine as defined in mammals, as teeth situated between the lateral incisors and the first premolar), and posterior cheek teeth that are not replaced because they are acrodont. There is no differentiation of incisors, canines, premolars and molars in lizards, although some lizards are heterodont; for example, some teiids display a combination of canine-like anterior teeth and enlarged crushing cheek teeth (see Estes & Williams 1984). These teeth are better termed caniniforms and molariforms, rather than canines and molars. Similar use of terms as Smith's is seen in Gilmore (1943a: "incisors", "canines", and "last molar"), Harris (1963, 1964: "incisor of rainbow lizard"), Estes & Williams (1984: "molar hypertrophy" and "molar expansion"). Applying these terms to the dentition of lizards is incorrect and should be avoided.

"Dental formula": Some authors (Gilmore 1926, 1928, 1942b; Presch 1970, 1974b; Sulimski 1975) inappropriately refer to a dental formula in systematic descriptions of, or even in diagnoses, of lizard taxa. A dental formula is the formula that expresses mammalian heterodonty, that is, the numbers of each category of teeth for a given taxon of mammals (Barghusen & Hopson 1979; Carroll 1988). Accordingly, a dental formula is used for mammals because, generally speaking, both tooth number and tooth form for a mammalian species are invariably stable, with a fixed number of tooth type (e.g., incisors, canines) and a fixed number of positions or loci along the tooth row. The lizard dentition is not the same. Since the marginal teeth of lizards are not differentiated into incisors, canines, premolars, and molars, use of a dental formula for lizards is inappropriate.

Furthermore, the dentition of lizards is not static as in mammals: Owing to rapid (and sometimes irregular) tooth replacement, along with ontogenetic changes in the length of tooth row, the number of marginal teeth in lizards is individually variable in the same species. Ray (1965) pointed out that the number of tooth positions in lizards is largely correlated with size, and size is mainly an ontogenetic or sex character. Edmund (1969, tables I-VIII) demonstrated that tooth number is quite variable in different individuals of the same species (e.g., dentary teeth of *Iguana iguana* vary from 17 to 29, depending on differences of size and age). MacLean (1974) provided comparable data for dentary tooth counts in microteiids (*Ptychoglossus* 15-35; *Alopoglossus* 18-32; *Placosoma* 17-18; *Argalia* 18-19). Thus, tooth count alone is nondiagnostic for lizard taxa. However, in combination with tooth form and other characters, tooth count is broadly useful in comparison of closely related species of lizards. Nevertheless, unless the ontogenetic change is well-understood, using tooth count to diagnose lizard taxa should be avoided.

SYSTEMATIC PALEONTOLOGY

Class Reptilia Linnaeus 1758
Subclass Diapsida Osborn 1903
Infraclass Lepidosauromorpha Benton 1983
Superorder Lepidosauria Haeckel 1866
Order Squamata Oppel 1811
Suborder Lacertilia Owen 1842

The suborder Lacertilia is a paraphyletic group by cladistic definition, as the suborder includes lizards, but not amphisbaenians and snakes, which are highly specialized squamates sharing a common ancestor with lizards. Rage (1982) made an effort to establish cladistic monophyly of the Lacertilia, but failed because all three of his presumed synapomorphies are either invalid or questionable (Estes et al. 1988). Because the cladistic monophyly of the Lacertilia cannot be established, Estes et al. (1988) recommend abandonment of this term (also see Rieppel 1988). The term "Sauria", commonly used as a synonym of Lacertilia by other authors, has been recently defined in a very different way, as a name for a higher taxon including both Archosauromorpha and Lepidosauromorpha (Gauthier 1984; Gauthier et al. 1988).

"Lacertilia" is used in this paper as a taxonomic term for "lizards" as traditionally employed (see, e.g., Camp 1923; Romer 1956; Robinson 1967; Carroll 1988), since a formal, cladistic diagnosis of lizards has not been achieved. There have been suggestions (Estes et al. 1988; Rieppel 1988) to classify Iguania and Scleroglossa (including amphisbaeneans and snakes) as equal taxa; however, the higher classification of the squamates is beyond the scope of this paper and is not considered further here.

Infraorder Iguania Cuvier 1807

Family Iguanidae Gray 1827

Genus Cnephasaurus n. gen.

Type and only known species: Cnephasaurus locustus n. sp.

Range: Upper Cretaceous, North America.

Diagnosis: As for the type and only known species.

Etymology: knephas + sauros (Gr. m.), meaning twilight lizard; this lizard may have been active at twilight hunting for grasshoppers, by analogy with its presumed relative, Recent Crotaphytus.

Cnephasaurus locustus n. sp.

Plate 1, Figs. 1-3; Text-fig. 3

Holotype: UALVP 29921, a right maxillary having 11 well-preserved teeth and broken bases for three others.

Type locality and horizon: MR-6 locality, Verdigris Coulee, about 30 km east of the village of Milk River, southern Alberta; upper member of the Upper Cretaceous Milk River Formation (Aquilan in age).

Referred specimen: UALVP 33386, topotypic left maxillary with four teeth and broken bases for two others.

Known distribution: Known only from the type locality and horizon.

Diagnosis: An early Campanian small iguanid, closely resembling Recent Crotaphytus in having highly heterodont dentition, but differing from the latter as follows: premaxillary process much shorter, nasal process unretracted, posterior palatal process on supradental shelf lacking.

Etymology: locusta (L.), grasshopper; the diet of this lizard may have consisted largely of grasshoppers, judging from its dentition.

Description: The holotype maxillary (UALVP 29921) is small and delicately built, having a total length of about 8 mm. The specimen is anteriorly complete, but broken dorsally and posteriorly; the nasal process is missing and the tooth row is incomplete. Anteriorly, both the lateral and the medial premaxillary processes are short and delicate, and not clearly divergent from each other. The anterior interior alveolar foramen is as small as the lateral superior alveolar foramina and opens above the base of the premaxillary processes.

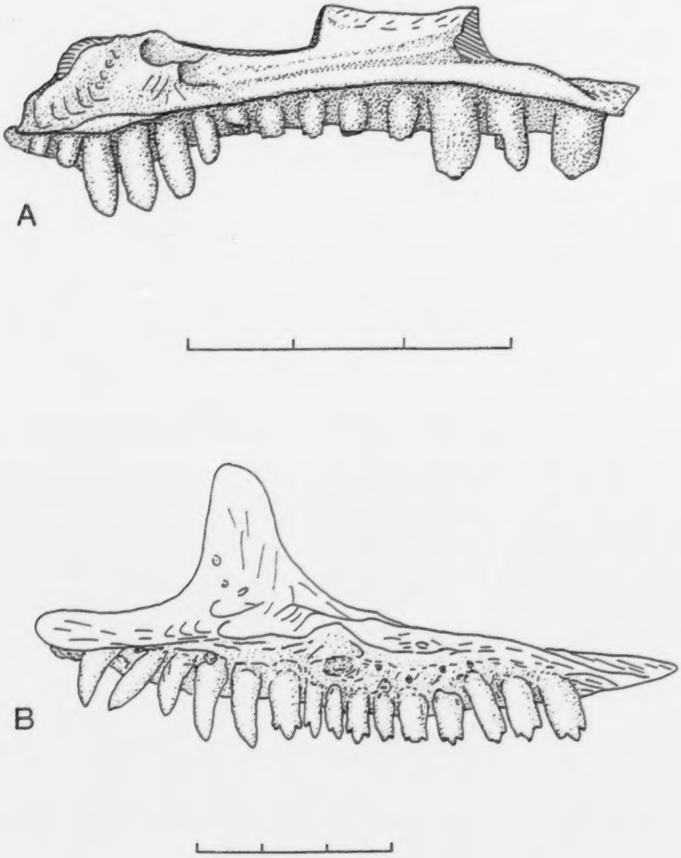
Medially, the holotype bears a slender but clearly defined supradental shelf, the medial border of which is straight in dorsal view, owing to the lack of a palatal process. No definite supradental gutter can be recognized. Anteriorly above the supradental shelf is a small pocket-like notch that probably received the lateral process of the palatine. Posteriorly, a comparatively large posterior interior alveolar foramen opens above the 12th tooth position. This is a generalized condition in comparison to Crotaphytus, in which this foramen opens anteriorly internal to the nasal process, shortly behind the anterior interior alveolar foramen.

UALVP 29921 has 14 tooth positions preserved, including 11 teeth and the broken bases of three others. With probably the two posteriormost teeth missing, a complete count is estimated at about 16. The maxillary tooth row is strongly heterodont: the first two teeth are broken, but were apparently slender and procumbent; the following three are clearly cylindrical and unicuspid; the sixth tooth is much reduced in size but still remains as cylindrical and unicuspid as the more anterior ones. This tooth is followed by five even shorter and stouter middle teeth, the crowns of which are slightly laterally compressed and medially concave. Behind these are three enlarged teeth, with one or two posteriormost teeth missing. Both the middle and posterior teeth are broadly based and tricuspid (or incipiently tricuspid), but the posterior ones are much larger and more robust, and strongly separated from the smaller middle ones by an abrupt jump in size along the tooth row. Corresponding to the heterodonty of the maxillary teeth, the spacing between the tooth positions is also variable along the tooth row: the anterior unicuspid teeth are closely spaced and the middle and the posterior tricuspid teeth are more widely spaced from one another. No replacement pits or basal foramina can be seen on this specimen.

The lateral surface of the maxillary is smooth, with no osteodermal incrustation. Six superior alveolar foramina, all small and rounded, are spaced equally except for the anteriormost two, which are closer together. The posteriormost foramen, which is usually associated with the posterior interior alveolar foramen, is located close to the posterior end of the maxillary, in this respect differing from that in Crotaphytus, in which the foramen is located lateral to the nasal process and anterior to the midpoint of the tooth row. The nasal process of the maxillary is mostly broken off, but the dorsal border posterior to the nasal process and above the last three superior alveolar foramina is preserved; this border clearly indicates that the nasal process descended sharply anterior to the midpoint of the tooth row; therefore, the nasal process is located anteriorly in front of the midpoint of the tooth row. An incomplete survey of this character state among Recent lizards indicates that this condition is probably unique to iguanians.

Discussion: Cnephasaurus locustus is principally based on a small maxillary, UALVP 29921. In addition, UALVP 33386, a maxillary fragment of similar size and having the same tooth form is also referrable to this species; it, too, is from the MR-6 locality. This new lizard from the upper member of the Milk River Formation has the nasal process located in front of the midpoint of tooth row, and a pleurodont dentition. The combination of these two characters indicates that the lizard is a non-acrodontan iguanian; thus, it is referrable to the Iguanidae. In addition, its close resemblance in dentition to Crotaphytus strongly supports this referral.

Perhaps the most unusual characteristic of this lizard is the regional differentiation of the tooth form accompanied by a sharp change of tooth size. As described above, the tooth row of this species consists of six slender, high-crowned and unicuspid anterior teeth, followed by five or so "pygmy" and incipiently tricuspid middle teeth, and then the enlarged posterior teeth. Both the holotype and referred maxillary have the same pattern of size change with no replacement pits shown on these specimens, suggesting that this pattern of heterodonty is taxonomically significant. An alternative explanation might be that both specimens are from young individuals that have not reached the stage for tooth replacement, and the small size of the middle teeth reflects retarded development at an early postembryonic stage. Nevertheless, since the two specimens show the same condition, the first alternative seems preferable. It is interesting to note that an astonishingly similar condition is seen in Recent Crotaphytus collaris Say 1823 (see Text-fig. 3 for comparison), the dentition of which, according to Hotton (1955), is adapted for feeding on highly active grasshoppers, having an integument of intermediate weight. Although the homology of this similarity can not be tested at present, Crotaphytus is indeed the only group that shows this character. This similarity may indicate a close affinity of the Milk River new iguanid to the Crotaphytinae Smith & Brodie 1982. However, this assumption cannot be fully verified until more extensive evidence is found.



Text-fig. 3. Iguanidae, comparison of holotype of *Cnephasaurus* *locustus* n. gen. et sp. and *Crotaphytus* *collaris*. A - holotype (UALVP 29921) of *C*. *locustus*, right maxillary, medial view; upper member of Milk River Formation, southern Alberta. B - right maxillary of *Cr*. *collaris*, medial view. Scale = 5 mm.

Recognition of Cnephasaurus locustus as an early iguanid is of both taxonomical and biogeographical significance. Taxonomically, this new taxon documents the earliest fossil record of the family Iguanidae, as the Milk River Formation is of early Campanian age (L. S. Russell 1964, 1975; Fox 1976; Lillegraven & McKenna 1986; Lillegraven 1991), some 18 Myr. (Harland et al. 1990) earlier than the supposed Maestrichtian Pristiguana Estes & Price 1973 from Brazil. Biogeographically, it marks the first discovery of Mesozoic iguanids from North America, which was part of the northern landmass during the Cretaceous. It has been suggested that the family Iguanidae originated in South America some time in the latest Jurassic (Estes 1983a-b; Estes & Price 1973; Estes & Baez 1985) and did not reach North America until middle Paleocene or early Eocene (Sullivan 1982; Estes & Baez 1985). The new discovery of early Campanian iguanids from North America, coupled with recent discoveries of a slightly younger fossil record of the same group from the Central Asian Gobi Desert (Borsuk-Bialynicka 1991; Gao & Hou 1992), indicates the presence of iguanids in North America and Central Asia well before they occurred in South America in the latest Cretaceous or Paleocene (Estes & Price 1973; de Muizon et al. 1983). The early geological age and primitive morphology of these iguanids strongly challenge the South American origin hypothesis, and suggest a northern continental origin of the family.

Iguanidae, genus & species new (A)

Plate 1, Figs. 4-6; Text-fig. 4

Specimens: UALVP 29908, left maxillary fragment with three well preserved teeth and the base of another; UALVP 29909, left dentary fragment with two teeth and the space for another.

Locality and horizon: MR-6 locality, Verdigris Coulee, approximately 30 km east of the village of Milk River, southern Alberta; upper member of the Upper Cretaceous Milk River Formation (Aquilan in age).

Description: UALVP 29908 is a left maxillary fragment that is both anteriorly and posteriorly broken. The facial process is largely missing, but the preserved posteroventral part is vertically straight, indicating the process in this species is high. The posterodorsal edge of the maxillary fragment is a natural border (not a broken surface), representing the descent of the maxillary posterior to the facial process. This specimen also shows that the lateral surface of the maxillary is smooth, bearing relatively large superior alveolar foramina (one shown on this specimen).

Medially, UALVP 29908 shows a thin and slender supradental shelf, which has no dental gutter. Dorsal to the shelf is the narrow opening of the posterior interior alveolar foramen. This foramen usually opens at the posterior part of the tooth row, and the inclined dorsal edge above it clearly indicates that the specimen represents the posterior part of the maxillary.

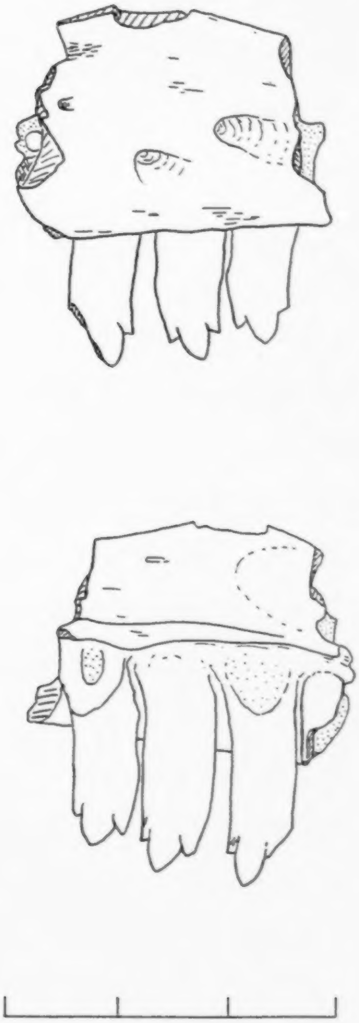
UALVP 29908 bears three well-preserved teeth, which are high-crowned, and pleurodont, with half of their height attached to the lateral parapet of the jaw. The teeth are basically cylindrical, but are concave medially with the crowns slightly bent lingually. The crowns are tricuspid, having a strongly prominent central cusp and much weaker but clearly defined anterior and posterior side cusps. The crowns are slightly twisted, so that the three cusps are aligned at an angle of approximately 45 degrees to the tooth row, and the central cusp is curved medioposteriorly. The anterior accessory cusp is slightly stronger than the posterior one.

A dentary fragment (UALVP 29909) from the same locality has two teeth preserved, one complete and the other with the crown broken off. The central and anterior cusps are similar to those on the maxillary (UALVP 29908), but the tooth lacks a clearly defined posterior cusp, a condition that can be termed either bicuspid or incipiently tricuspid. It seems likely that the differences in the development of these cusps are relevant to tooth position, with the posterior teeth having strongly tricuspid crowns. However, this interpretation cannot be verified until more nearly complete specimens of this species are recovered. Because of the fragmentary nature of the specimens, the possibility of the second specimen representing another species cannot be ruled out.

Discussion: The new genus and species (A) is recognized principally on UALVP 29908, while the other specimen (UALVP 29909) is referred to the same species with some uncertainty. Although fragmentary, UALVP 29908 clearly shows that at least the middle-posterior teeth of this lizard are definitely tricuspid, with the central cusp being much higher than the lateral ones, and the crowns twisted at a 45 degree angle to the straight line of the tooth row. This particular cusp pattern in association with other characters, such as crown height and mode of tooth attachment, provides useful imformation concerning its taxonomic placement at a familial level.

Tricuspid teeth are commonly seen in Teiidae, Iguanidae, and are also in some genera of Xantusiidae (Savage 1963). In tricuspid teiid teeth, the three cusps are characteristically more or less equal in height, a pattern that is often closely associated with other characters, such as subpleurodonty, and a well-developed dental shelf and dental gutter (see Estes 1964, 1983a; Presch 1970; Gao & Fox 1991). All of these features are different from the condition seen in UALVP 29908, excluding the possibility of its affinity to the family Teiidae, which is greatly diverse in the North American Upper Cretaceous. Two genera of Xantusiidae (Klauberina and Lepidophyma) are known to have tricuspid teeth (Savage 1963), but the tricuspid condition in UALVP 29908 is obviously different from that of the xantusiids: in xantusiids, the two side cusps are more lingually located than the central cusp ("anterior and posterior cusps on inner surface of teeth", Savage 1963: 30).

UALVP 29908 has an interesting combination of high-crowned, tricuspid, and highly pleurodont teeth, while lacking a dental gutter. This combination of characters indicates that the specimen is referrable to the family Iguanidae. The teeth of iguanids are generally high-crowned and pleurodont, and with more or less flared crowns that can be either tricuspid or polycuspid (having four or more cusps). The tricuspid condition in the Iguanidae is commonly characterized by having "a large apical cusp, smaller anterior and posterior cusps, and more or less parallel sides" (Etheridge & de Queiroz 1988: 297). Recent cladistic analysis of iguanid phylogeny indicates that tricuspid tooth form is a primitive condition in the family Iguanidae (Etheridge & de Queiroz 1988). Thus, UALVP 29908 may represent another primitive and one of the earliest known iguanids from the Milk River Formation. However, the specimen is too fragmentary to show the nature of the premaxillary and facial processes, making a comparison with Recent specimens impossible.



Text-fig. 4. Iguanidae, genus & species new (A), upper member of Milk River Formation, southern Alberta; UALVP 29908, fragmentary left maxillary; (above) lateral view, (below) medial view. Scale = 3 mm.

Iguanidae, genus & species new (B)

Plate 1, Figs. 7-10; Text-fig. 5

Specimens: SMNH P1927.916, dentary fragment bearing five teeth and the base of another; SMNH P1927.885, left dentary fragment bearing four teeth and the bases of two others; SMNH P1927.998, right dentary fragment with three teeth and the base of another. SMNH P1927.980, dentary fragment bearing four well-preserved teeth.

Locality and horizon: Gryde locality, in Sec. 19, Tp. 4, R. 18, W. 3, Frenchman Valley, southwestern Saskatchewan; Upper Cretaceous Frenchman Formation (Lancian).

Description: SMNH P1927.916 is a fragmentary tooth-bearing dentary, which is obviously from a small individual, as shown by the size of the specimen. Although fragmentary, the specimen shows that the subdental shelf is poorly defined and has no dental gutter (sulcus dentalis). The lower portion of the jaw fragment is missing, providing no information about the splenial bone, splenodentary articulation, and the Meckelian canal.

The dentary fragment bears five teeth and the base for another. The five teeth are complete or nearly complete; only the last on the specimen is badly broken. These teeth are high-crowned and pleurodont, with the lower half of the teeth attached to the lateral parapet of the jaw. The tooth crowns are flared, slightly recurved, and tricuspid, having a highly prominent main cusp and two much lower side cusps. The side cusps are clearly separated from the central main cusp, and each has a vertically-running ridge on the medial surface of the crown. The anterior side cusp is slightly stronger than the posterior one on each tooth. The tooth shafts are slenderly cylindrical and are closely packed along the tooth row. The tooth bases are slightly thicker than the shafts and show no sign of tooth replacement on the specimen.

SMNH P1927.885, a left dentary fragment, has four teeth and the spaces for two others preserved. The teeth are high-crowned, pleurodont, and the cylindrical tooth shafts are slightly curved. The tooth crowns are not well-preserved, but apparently tricuspid. The subdental shelf is slightly stronger than on the other three specimens, and it seems to bear a poorly defined sulcus dentalis.

SMNH P1927.998 is the fragment of a small right dentary, which bears three teeth (one complete and the other two with the crowns broken off) and the space for another. The tooth form of this specimen is similar to that of SMNH P1927.916, that is, slender, cylindrical, and tricuspid, and the subdental shelf is weak with no sulcus dentalis. The Meckelian canal is extremely restricted, opening narrowly ventromedially, indicating a greatly reduced splenial. The lateral surface of the jaw fragment is smooth, relatively flat, and bears two mental foramina that are widely separated from each other by four tooth positions.

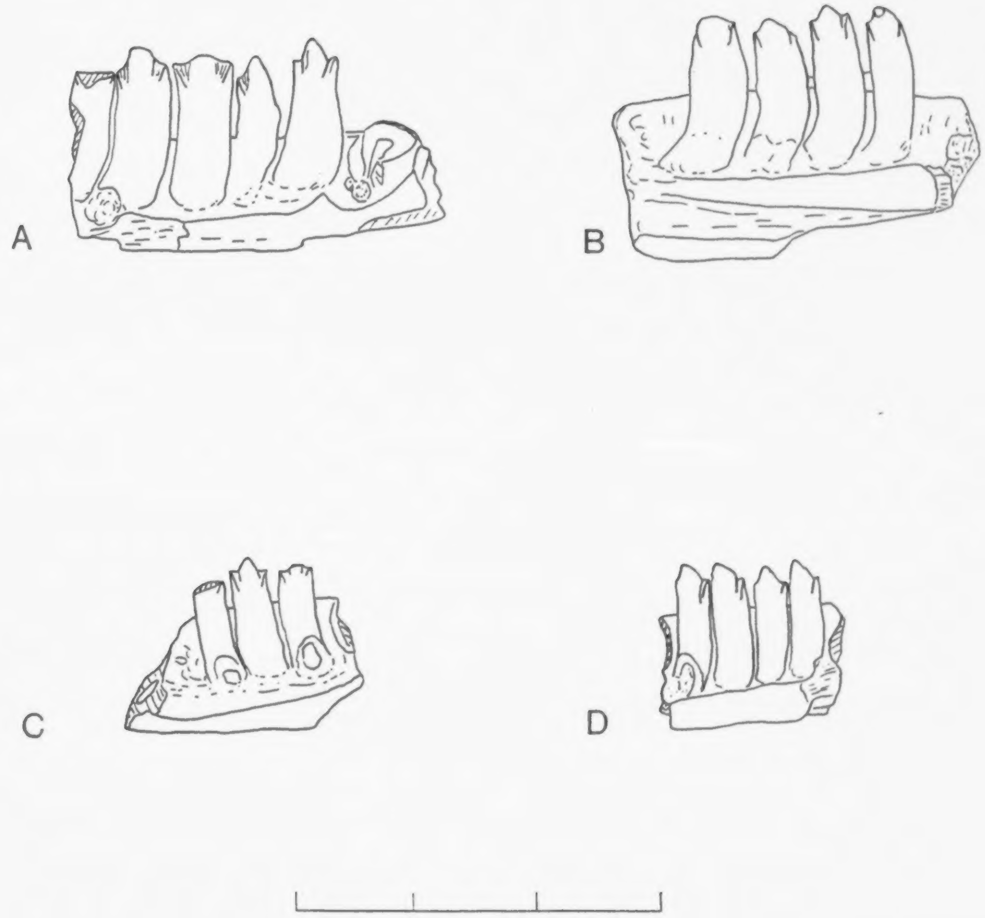
SMNH P1927.980 is a left dentary fragment bearing four well-preserved teeth. Like SMNH P1927.916, this fragment shows a weakly developed subdental shelf, and high-crowned and pleurodont teeth closely spaced from one another along the tooth row. The tooth shafts are slender, cylindrical, and the crowns are flared and slightly recurved. However, the tooth crowns of this specimen are clearly bicuspid, differing from the tricuspid condition on SMNH P1927.916. Owing to the incompleteness of the two specimens, I am unable to determine whether the difference of the crown pattern is taxonomically significant, or simply that the two specimens are from a different portion of the dentary tooth row. Therefore, its referral together with other three specimens to the same unnamed taxon is tentative.

Discussion: Whereas the four specimens described above are too fragmentary to show the general jaw configuration, the tooth form of these specimens is especially interesting, indicating the presence of at least one new genus and new species previously unknown from Lancian horizons. However, the new lizard is unnamed in this study because the available specimens are inadequate to show diagnostic characters other than tooth form; jaw structure, such as the morphology of the splenial, is important in determining taxonomic position.

Although this new genus and new species remains unnamed (thus no holotype is designated), SMNH P1927.916 is the specimen based on which the new taxon is recognized. It clearly shows tall teeth having flared and tricuspid crowns, a poorly defined subdental shelf, and no sulcus dentalis. These are derived character states that in combination strongly indicate the affinity of this lizard to the family Iguanidae. Within the Iguanidae, the closest resemblance in terms of tooth morphology of this Lancian form is to Ctenosaura (e.g., C. similis Gray 1831, see Ray 1965, fig. 5), which has a geographical distribution in Mexico and Central America (Estes 1983a). According to Hotton (1955), C. similis is chiefly herbivorous, but its diet also includes insects at times.

SMNH P1927.998 is an important specimen as it shows strong evidence of iguanid affinities: the total loss of the sulcus dentalis, greatly reduced splenial as indicated by the extremely narrow Meckelian canal, highly pleurodont dentary teeth with tricuspid crowns, and direct tooth replacement as suggested by the absorption pits at the medial side of the tooth bases. However, I am unable to determine if this specimen can be put with P1927.916 and P1927.885 in the same species, as the teeth of this jaw fragment are less high-crowned and less flared than those of the two specimens mentioned above. I tentatively put them together on the basis of their tricuspid crown pattern, regarding the differences in tooth height as related to regional variation along the tooth row.

SMNH P1927.980 is similar to P1927.916 in having high-crowned, cylindrical teeth with flared crowns, but differs from the latter in having a bicuspid rather than tricuspid crown pattern. It is closely similar to P1927.916 in every aspect but lacks a posterior side cusp on the crowns. At this stage, I am unable to determine whether this difference is taxonomically significant, or simply reflects differences in cusp pattern along the different parts of the tooth row.



Text-fig. 5. Iguanidae, genus & species new (B), Frenchman Formation, Saskatchewan; A - SMNH P1927.916, fragmentary left dentary; B - SMNH P1927.885, fragmentary left dentary; C - SMNH P1927.998, fragmentary right dentary; D - SMNH P1927.980, fragmentary left dentary. Scale = 3 mm.

From the above discussion, the four specimens from the Upper Cretaceous Frenchman Formation represent at least one (and maybe more than one) new taxon that is likely associated with the family Iguanidae in terms of tooth form and implantation. The four specimens are referred to the same unnamed taxon on the basis of their general similarity in tooth form and their origin from the same locality. SMNH P1927.916 and P1927.885 are clearly the same kind, whereas P1927.980 and P1927.998 seem to less clearly resemble the former two specimens in terms of crown pattern (number of cusps), but cannot be determined to be a separate taxon at the present time.

Infraorder Scincomorpha Camp 1923

Superfamily Lacertiformes Estes et al. 1988

Family Teiidae Gray 1827 (sensu Estes 1983a; Presch 1983)

Boulenger (1885) subdivided the Teiidae (sensu lato) into four major groups (I-IV). His group I was later informally known as "macroteiids" and group II as "microteiids" (Ruibal 1952). MacLean (1974) recognized the two groups as separate subfamilies (Teiinae and Gymnophthalminae). More recently, Estes (1983a) and Presch (1983) independently ranked the two groups as families. "Teiidae" (sensu stricto) as used in this paper refers to Boulenger's group I (macroteiids) in the sense of Estes' (1983a) and Presch's (1983) definition. In the most recent study of the phylogenetic relationships of the lizard families, Estes et al. (1988) listed 14 synapomorphies for the family Teiidae, among which the following are unambiguous and reliable character states for fossil teiid studies: replacement teeth developing in deep subcircular cavities at tooth bases (Romer 1956); cementum deposited extensively on tooth bases (Presch 1974b); vomer elongated, approaching pterygoid (Romer 1956); splenial hypertrophied, extending anteriorly to the symphysis leaving only a small symphysial foramen (MacLean 1974). So far, the earliest known fossil record of this family comes from the Comanchean of Texas (Winkler et al. 1990).

Genus Chamops Marsh 1892

Type species: Chamops segnis Marsh 1892.

Range: Upper Cretaceous, North America.

Diagnosis (revised from Estes 1983a): Late Cretaceous teiid close to Recent Callopistes Gravenhorst 1838, but differing from the latter and other living or fossil teiid species in having the following combination of character states: dentary short and robust, with weak mandibular symphysis; tooth row weakly heterodont, having low-crowned teeth with broadly tricuspid crown, swollen shaft, and heavily cemented base.

Chamops segnis Marsh 1892 (emend. Gilmore 1928; Estes 1964, 1983a)

Plate 2, Figs. 1-5; Text-fig. 6

Holotype: YUM 1036, a fragmentary left dentary with five well-preserved teeth, from the Lance Formation, Niobrara County, Wyoming. The holotype was originally identified by O. C. Marsh (1892) as a right maxillary; the identification was erroneous and was later corrected by Estes (1964).

Referred specimens: Frenchman Formation, Gryde locality: SMNH P1927.824-825, P1927.831, P1927.876, P1927.882, P1927.899, P1927.966, P1927.969, P1927.993, P2004.86 (total: 10), incomplete maxillaries; P1927.827, P1927.874, P1927.883, P1927.890, P1927.920, P1927.991 (total: 6), fragmentary dentaries. Wounded Knee locality: UALVP 29731, incomplete maxillary; UALVP 29728, 29811-29812, fragmentary dentaries.

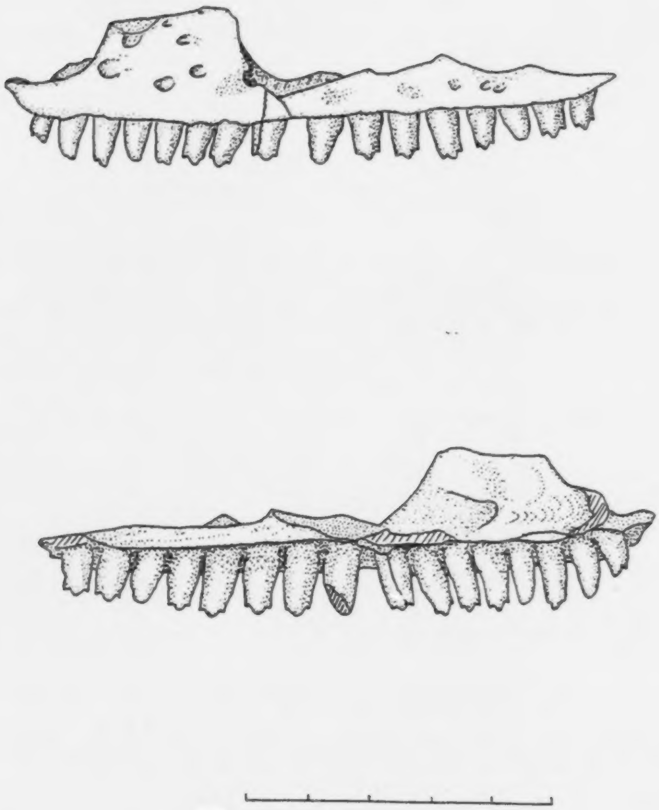
Scollard Formation, KUA-1 locality: UALVP 29841, fragmentary maxillary; KUA-3 locality: UALVP 29842-29843, incomplete dentaries.

Known distribution: Upper Cretaceous Lance Formation, eastern Wyoming; Hell Creek Formation, eastern Montana; Scollard Formation, central Alberta; and Frenchman Formation, southwestern Saskatchewan (all Lancian in age).

Diagnosis: Large North American Lancian teiid; differing from Callopistes maculatus Gracenhorst 1838, the closest living species, in having the following combination of character states: tooth row weakly heterodont, with anterior teeth conical and posterior teeth tricuspid; marginal teeth low-crowned, swollen, and bottle-shaped.

Description: Among the specimens used in this study, more than 30 maxillaries and dentaries can be confidently identified as Chamops segnis, on the basis of tooth morphology and jaw configuration. The following description is based on several relatively well-preserved maxillaries and dentaries in the collections available for this study.

Maxillary.-SMNH P2004.86 (Text-fig. 6) is the left maxillary of a young individual, judging from its small size (about half size of UCMP 46033, see Estes 1964, fig. 47). The maxillary has part of its dorsal process broken away; otherwise it is complete. It has a short premaxillary process, behind which the nasal process rises abruptly as a vertical lateral wall, as in UCMP 46033, a maxillary from the Lance Formation (see Estes 1964, fig. 47). Medially, the maxillary bears a well-developed supradental shelf, the medial edge of which is nearly straight, and lacks a palatine process. The posterior interior alveolar foramen opens above the shelf at a position between the fifth and the sixth most posterior teeth. The full maxillary tooth row is preserved on this specimen and contains 16 short-crowned teeth with swollen shafts. The first four anterior teeth are conical (with lateral ridges) and are slightly recurved; the next three are weakly tricuspid, while the rest are broadly tricuspid.



Text-fig. 6. Teiidae, *Chamops segnis*, Frenchman Formation, southwestern Saskatchewan; SMNH P2004.86, incomplete left maxillary; (above) lateral view, (below) medial view. Scale = 5 mm.

The crown pattern of the maxillary teeth is best shown on SMNH P1927.824 (Pl. 2, Fig. 2), an incomplete left maxillary of the same size as SMNH P2004.86 described above. The specimen has 14 tooth positions (12 teeth + bases of two others), with probably the most anterior two teeth broken away. In SMNH P1927.824, the tricuspid condition of the maxillary teeth starts from the fifth anterior tooth, and the middle and posterior teeth are short, broadly tricuspid, and slightly concave medially. The third most posterior tooth on this specimen is medially offset from the tooth row, and the crown is bent laterally; obviously, this is the result of pathologic development of the tooth. Tooth implantation is subpleurodont. A shallow sulcus separates the tooth row from the supradental ridge. As commonly seen in other specimens of the species, the maxillary teeth are moderately spaced from one another, and are slightly concave on the lingual surface. The teeth have a basal deposit of cementum, but it is obviously much less heavy than on larger specimens in the collection. The small size of the maxillary, plus its weakly developed basal cementum, imply that this maxillary is from a young individual.

Dentary.-In this study, 11 dentaries from the Frenchman and Scollard formations are referred to Chamops segnis on the basis of tooth form and jaw structure; the best preserved of these are described as follows:

SMNH P1927.874 is an incomplete right dentary bearing 11 tooth positions (eight teeth and the bases of three others). Collected from the Gryde locality of the Frenchman Formation, the dentary is small, indicating a young individual. Although most of the lateral wall of the Meckelian canal is missing by breakage, the tooth form and the parts of the dentary that remain provide reliable characters for identification. Medially, the dentary bears a strong subdental shelf, the anterior end of which forms part of the weak mandibular symphysis. The first five to six teeth are slender, conical, and slightly procumbent; and the remainder of the teeth strongly increase in size posteriorly. Most of these teeth are poorly preserved, but the tricuspid crown pattern is clearly shown on the eighth tooth position. In spite of the small size of the specimen, tooth replacement is shown at the sixth and the tenth positions, where the remaining bases of the replaced teeth still can be seen. In dorsal view, the tooth row is straight, lacking the curvature seen in Leptochamops Estes 1964, another teiid lizard from the same horizon.

Generally speaking, the dentary of Chamops segnis is short and robust, but it has a weak symphysis; it differs from the dentary of Leptochamops in having a much wider Meckelian sulcus, much deeper boat-shaped ventral curvature, straight subdental shelf, and a posterior interior alveolar foramen that opens under the twelfth tooth. In addition, the dentary external surface of Chamops is smoothly convex dorsoventrally, lacking the labial concavity seen in Leptochamops denticulatus (Gilmore 1928) Estes 1964.

The tooth row is weakly heterodont: the anterior four teeth are conical; these are followed by a few weakly tricuspid teeth, and then by widely tricuspid posterior teeth with short and swollen shafts. Estes (1964) stated that the incipiently tricuspid anterior teeth are separated from the posterior ones by a "step" (see discussion on p. 49). Estes (1964) also stated that the dentary tooth count of Chamops segnis is 18 on the basis of UCMP 49881, which shows the complete tooth row. Among the specimens used in this study, no dentary contains the full tooth row; the highest number of preserved tooth positions is 11, as shown on SMNH P1927.874 from the Frenchman Formation, Saskatchewan.

In addition to the specimens that are described or mentioned above, several tooth-bearing maxillaries and dentaries of the same species, but from the Lance and Hell Creek formations are also included in this study. These specimens clearly show individual variation in certain features of the tooth row (see discussion below). These Lance and Hell Creek specimens include: UALVP 29727, 29729, 29813 (maxillaries), and 29814 (dentary) from the BTB locality of the Lance Formation, Wyoming; and UALVP 29724-29726, 29730, 29737-29738 (maxillaries), 29721, 29723, and 29815 (dentaries) from the BCA locality, Hell Creek Formation, Montana.

Discussion: *Chamops segnis* is a common North American Late Cretaceous species, fossils of which have been collected from all major Lancian formations in the Western Interior. *Chamops segnis* has also been reported from the Wapiti Formation (Sternberg 1951), Oldman Formation (Waldman 1970; Estes 1983a), and the Fruitland Formation (Armstrong-Ziegler 1978, 1980; Sullivan 1981), but a careful review of the materials indicates that these occurrences are unconvincing (see Gao & Fox 1991, and later discussion). Thus, *Chamops segnis* is a problematic species; in this study, problems bearing on its taxonomic history, diagnostic characters, synonyms, and its relationships with other lizards are treated in the following discussion.

1) Taxonomic History and Relationships of *Chamops segnis*

Chamops segnis was originally named by O. C. Marsh (1892), based on several specimens collected by J. B. Hatcher in 1889 from the Lance Formation of eastern Wyoming. In his paper entitled "Notice of new Reptiles from the Laramie Formation", Marsh designated a left dentary, misidentified as a maxillary, as the type specimen, but provided no specimen number, no morphological description, and no diagnostic characters for the new genus and species. It was not until 1928, when Gilmore gave a detailed description of Marsh's type specimen and pointed out its diagnositc characters, that *Chamops segnis* became a fully established taxonomic name.

It also should be noted that Gilmore (1928) followed Marsh's incorrect identification, and described the type specimen (YUM 1036) as a maxillary rather than a dentary. Estes (1964) was the first to note that Marsh's identification of the type specimen of *Chamops segnis* as a maxillary is incorrect. He (Estes 1964, pl. 2) provided a clear photograph of the type specimen, which shows five (rather than ten) complete dentary teeth and the tooth bases of five others. This condition of the specimen is consistent with Gilmore's (1928: 24) description, but different from Marsh's (1892, fig. 2-3) original figures that show nine complete teeth and the base of another. Therefore, it may be that between 1892 and 1928 the type specimen was damaged, with four teeth broken and lost.

Marsh (1892) did not discuss the relationship of Chamops segnis with other lizards. Subsequently, the species was referred to the Teiidae by Boulenger (1892) and Nopcsa (1908) without comment, and was placed in the Iguanidae by Hay (1902), Camp (1923), and Gilmore (1928). Estes (1964) noted that "Chamops differs in many ways from known iguanids, principally in the broadly open Meckelian fossa, the concomitantly large splenial, and less pleurodont implantation of teeth". Recognizing the significant similarities to the Recent teiids Crocodilurus lacertinus (Daudin 1802) Dumeril & Bibron 1839, and Tupinambis nigropunctatus Spix 1825, Estes placed Chamops in the Teiidae. Subsequently, he (Estes 1969a, 1983a) further recognized that the closest relationship of Chamops segnis is with Callopistes maculatus, on the basis of similarity of maxillary, nasal, quadrate and parietal bones. The maxillary that Estes used for comparison (UCMP 46033) is restored dorsally from UCMP 46094, and "the parietals and quadrates are referred to Chamops on the basis of both size and frequency, as well as on their generally teiid appearance" (Estes 1969a: 5). The specimens used in this study add no further information as to the reliability of the association of these disarticulated skull elements; however, the relationship of Chamops segnis to the Teiidae can be determined without reference to skull elements, because teiid synapomorphies are clearly shown on the dentary specimens: these synapomorphies include: (1) large splenial, as indicated by the widely open Meckelian canal; (2) extensive basal deposit of cementum on the tooth bases; and (3) replacement teeth developing in deep subcircular basal cavities (see Estes et al. [1988] for citations). In addition, other characters, such as the subpleurodont tooth attachment, well-developed subdental shelf, and sulcus dentalis, are also indicative of the family Teiidae.

As Estes (1964, 1969a) noted, a character state shared between Chamops and Callopistes, but not with Crocodilurus Spix 1825 and Tupinambis Daudin 1803, is the relatively short face. In Callopistes, the upper jaw is shorter than one half of the total length of skull, while it is half, or often longer than half, the length of the skull in other teiids (see Presch 1970; pers. observ.). The short face is also consistent with a higher nasal process of the maxilla in Recent teiids (pers. observ.). Facial elongation is prominent in advanced teiids, such as Cnemidophorous Wagler 1830 and Ameiva Meyer 1795 (MacLean's [1974] "long-snouted species"). Thus, the deep maxilla and short face are probably primitive character states in teiids (Estes 1964).

2) Diagnostic Characters of Chamops segnis

As mentioned above, Marsh (1892) provided no diagnosis for Chamops segnis when he named the species. Gilmore (1928) was the first to diagnose the lizard as having "teeth pleurothecodont [subpleurodont]; internal and external surfaces of teeth grooved longitudinally; tricuspid; subequal in size; 23 teeth in complete dentary series" (Gilmore 1928: 24). However, his count of 23 dentary teeth was based on YUM 1062, a specimen apparently belonging to another genus and species (Leptochamops denticulatus Estes 1964). Actually, the full dentary tooth count of Chamops segnis is about 18, as Estes (1964: 102) described for UCMP 49881 and figured in UCMP 49871 (see Estes 1964, fig. 45).

Based on additional material collected from the Lance Formation during 1956-1958, Estes (1964) revised the diagnosis for the species as "a teiid lizard closely related to the living Crocodilurus lacertinus and Tupinambis nigropunctatus, differing principally from these in the less pronounced heterodonty, and less swollen tooth crowns; if the parietal is correctly referred, this species has a large parietal foramen, unlike all recent teiids" (Estes 1964: 102).

More recently, Estes (1983a) provided the latest version of the revised diagnosis for Chamops segnis: "teiid lizards apparently with a parietal foramen; tooth row very weakly heterodont, anterior teeth bicuspid or weakly triconodont, separated by an area of reduced tooth size from posterior triconodont teeth that have swollen bases and wrinkled crown surfaces; maxilla deep dorsoventrally; splenial very extensive, almost completely filling the widely open Meckelian sulcus" (Estes 1983a: 95). About this diagnosis, I offer the following comments.

First, the nature of the "area of reduced tooth size" ("step" in Estes 1964) is still unclear; however, it is individually variable within Chamops segnis, as the change in tooth size is not shown on the holotype YUM 1036 (see Marsh 1892, fig. 2-3; Estes 1964, pl. 2) nor on various other specimens. In the two best-preserved maxillaries (young individuals) from the Frenchman Formation, the "step" is present on SMNH P1927.824 but absent on the other (SMNH P2004.86). This variation is also shown in those large maxillaries from the Lance and Hell Creek formations collected by UALVP field parties: the step is present on UALVP 29729 (BTB locality), but absent on UALVP 29727 (BTB) and 29738 (BCA). Furthermore, as Estes (1964) showed, this "step" in the tooth row is also developed in some other teiids; for example, in living Crocodiluris lacertinus, Tupinambis nigropunctatus (see Estes 1964, fig. 48), and fossil Leptochamops denticulatus (see Estes 1964, fig. 50b, d). Therefore, the "area of reduced tooth size" or the "step" is not unique for Chamops segnis, and thus, cannot be regarded as a diagnostic character. It is difficult to evaluate this character without a complete survey of the dentition of teiids and related groups; however, it seems to me that the "step" is closely associated with the development of newly replaced teeth, suggesting a more frequent use of this part of the tooth row than of the others anterior or posterior to it. Functionally, the "step" may correspond to the biting mechanism of the jaws, that is, it may be the area frequently used to hold prey (insects). Estes et al. (1988: 162) regarded "a step in the maxillary tooth row to be a synapomorphy of Lacertiformes".

Second, as Estes noted, the referral of several parietals to Chamops segnis, including UCMP 57147 (figured in Estes 1964, fig. 49) is uncertain, because it is mainly "on the basis of size and frequency of occurrence" (Estes 1964: 104). There are other teiid species known from the same formation, and the specimens are disarticulated, being collected mostly by screen washing. Moreover, the size difference between Chamops segnis and other contemporaneous teiids is not great enough to separate the fragmentary skull elements one from another taxonomically. Therefore, it is diffcult to confirm the actual association of the disarticulated parietals with the jaw material of Chamops segnis, unless other evidence, such as a more or less complete skull, is discovered. Furthermore, even if a complete skull of Chamops segnis could be found and proved to have a parietal foramen, the presence of the foramen as a diagnostic character still is not warranted: other Cretaceous teiids, such as Polyglyphanodon Gilmore 1940 and closely related genera from Gobi Desert, clearly show a parietal foramen in the skull (Gilmore 1942b, 1943a; Sulimski 1972, 1975, 1978). Furthermore, ontogenetic evidence shows that loss of the foramen in most living species is a derived condition and must have been achieved quite recently in evolution (Presch 1970). Therefore, the presence of a parietal foramen in teiids is a primitive condition, and thus, should not be used as a diagnostic feature for any fossil species of teiids.

3) Synonyms

Estes (1964, 1983a) placed Iguanavus teres Marsh 1892, Lanceosaurus hatcheri Gilmore 1928, Lanceosaurus compressus Gilmore 1928 and Alethesaurus quadratus Gilmore 1928 in synonymy with Chamops segnis. I have compared the published data on these taxa (description, figures, and discussion) with those of Chamops segnis, and offer the following comments:

Estes (1964: 110) stated that "Marsh (1892, p. 309) described a nonanguimorph caudal vertebra from the Bridger Formation of Wyoming as Iguanavus exilis, and referred another caudal, from the Lance Formation, to another species, I. teres. This is figured by Gilmore (1928, pl. 2, fig. 1)." Unfortunately, this statement is incorrect: First, the original naming of Iguanavus exilis by Marsh was in 1872, twenty years earlier than 1892 when he named the second species I. teres. Second, Marsh (1872: 309) actually referred "a number of vertebrae, and a few other isolated specimens", rather than just one, to the Eocene species, I. exilis; it was Gilmore (1928) who selected the single caudal vertebra (YUM 1057) as the holotype. Third, Marsh (1892: 451) founded the Late Cretaceous species, I. teres, on his "type specimens" of dorsal vertebrae (rather than a caudal), from which Gilmore later selected YUM 530 as the type specimen (see Gilmore 1928: 17-18). The caudal that Estes (1964: 110) mentioned (GSC 2912) actually was collected by C. M. Sternberg in 1921, twenty-nine years later than Marsh's original naming of the species (Gilmore 1928, pl. 2, fig. 1), and was from Rocky Creek, Saskatchewan (originally cited as the Lance Formation by Gilmore, but now the Frenchman Formation, as named by Furnival in 1946).

As mentioned above, the species Iguanavus teres was named by Marsh (1892: 451) on several unnumbered vertebrae from the Lance Formation, Wyoming. Gilmore (1928) reviewed this species, and designated and described the type specimen, YUM 530. Gilmore's (1928) review apparently confirmed the presence of the genus Iguanavus in the Upper Cretaceous. However, Estes (1964, 1983a) put I. teres in synonymy with Chamops segnis on the basis of size and frequency of occurrence of the specimens. No vertebra has been found directly associated with diagnostic jaw material of Chamops, and the vertebrae of Chamops have never been described. Marsh's naming of Iguanavus teres based on only vertebral material is unfortunate, because vertebrae provide little information for species identification. Therefore, neither the validity of the name Iguanavus teres nor its synonomy with Chamops segnis can be confirmed. The species Iguanavus teres is based on specimens that are inadequate, probably non-diagnostic below the familial level; the type specimen (YUM 305) was never figured; and the species was never diagnosed. At least at this stage, Iguanavus teres is a "nomen dubium"; probably I. exilis (the type species) is, as well (Estes 1983a). Because Iguanavus teres was primarily founded on nondiagnostic material, it should also be regarded as a "nomen vanum" (sensu Simpson 1948; Mones 1989). A "nomen dubium" or a "nomen vanum" is an invalid name that has no standing in zoology (ICZN 1985; Mones 1989), although each stands as a nominal species in nomenclature (see Simpson 1948; Mones 1989).

Gilmore's (1928) Lanceosaurus included two species, Lanceosaurus hatcheri (type species) and L. compressus, both later placed as subjective synonyms of Chamops segnis by

Estes (1964). The type specimen of *L. hatcheri* (USNM 10706) is a left dentary containing partly dissolved teeth. Estes (1964) stressed the eroded nature of the type specimen and argued that a similar kind of erosion in some specimens of *Chamops* indicate they belong to the same genus and species. However, to synonymize *Lancesaurus* with *Chamops* is probably not a good practice in taxonomy, because USNM 10706 obviously differs from the dentary of *Chamops segnis* in having a more slender dentary, a much deeper subdental shelf and a more restricted Meckelian canal; further the degree of erosion of tooth crowns on the specimen is a taxonomically invalid character. Therefore, USNM 10706 should not be regarded as a jaw of *Chamops segnis*, and is so poorly preserved that it shows no characters adequate to establish a species. In view of this fact, *Lanceosaurus hatcheri* should be regarded as a "nomen dubium"; the name is invalid at present, but could be revalidated if sufficient specimens are found. The other species, *L. compressus*, displays a similar condition, and should be treated the same as the type species.

Gilmore's (1928) *Alethesaurus quadratus* was based on USNM 10802, a poorly preserved maxillary fragment "bearing four perfect teeth" as described (Gilmore 1928: 162), but there are actually only three and these are badly dissolved as photographed (see Gilmore 1928, pl. 26, fig. 13). "The manner of insertion and the general shape of the teeth resemble some of the posterior lateral teeth of *Tupinambis nigropunctatus*, suggesting possible affinities in the family Teiidae" (Gilmore 1928: 162). Estes (1964: 110) re-examined the holotype and concluded that the specimen was a well-worn dentary fragment of *Chamops segnis*, which bears the "last few teeth". I agree with Gilmore's original identification of the specimen as a maxillary fragment, as the dental shelf on the specimen is thin and plate-like, indicating a supradental shelf rather than a subdental shelf; however, *Alethesaurus quadratus* is in fact founded on an inadequate specimen that is generically and specifically non-diagnostic. Thus, in this study, I can neither re-validate the name, nor agree with Estes' placing it as a synonym of *Chamops segnis*. The posterior teeth of the latter species are widely tricuspid, and the tooth shafts are strongly swollen or "bottle-shaped"; none of these features are shown on the specimen USNM 10802, although Gilmore (1928: 162) mentioned "a vestigial denticle" at the base of the cutting edge of the teeth. The fragment shows no other jaw structures suggesting affinity to *Chamops segnis* or any other related species. In this paper, *Alethesaurus quadratus* is treated as a "nomen vanum", since it is "based on types which are inadequate for definitive diagnosis" (Mones 1989: 233). A "nomen vanum" has no standing in either zoology or nomenclature (ibid.), and cannot be synonymized with any other established taxon.

4) Problematic Reports and Misidentified Specimens

Chamops segnis is a common North American Late Cretaceous teiid, the geologic distribution of which is not known to extend beyond the K-T boundary (Fox 1989). This particular species is definitely known only from major Lancian deposits, including the Lance Formation, Wyoming (Marsh 1892; Gilmore 1928; Estes 1964, 1983a), Hell Creek Formation, Montana (Estes et al. 1969), Frenchman Formation, Saskatchewan (L. S. Russell 1964; Fox 1989), and now from the Scollard Formation, Alberta (this paper). There have been other reports of *Chamops segnis*, from geologically older horizons (see Estes 1983a: 95 for citations), but a careful review of the fossil record of this lizard indicates that these reports are unconvincing, based on either nondiagnostic or misidentified specimens.

C. M. Sternberg (1951) identified a lower jaw fragment (NMC 8891) as *Chamops* cf. [*C*.] *segnis* (incorrect syntax in using "cf.", see Lucas 1986 and Estes 1987 for comments, but also see Zidek 1987). The specimen was collected from the Upper Cretaceous Wapiti Formation (partially correlative to the Horseshoe Canyon Formation of central Alberta, see Tanke 1988, Dodson & Currie 1990) in the Kleskun Hills, near Grande Prairie, northwestern Alberta. Although the specimen was unavailable for this study, the original description and the illustration (C. M. Sternberg 1951: 256) show that NMC 8891 differs from *Chamops segnis* in having relatively high crowned and much less swollen teeth, as well as having a subdental shelf that sharply decreases in depth posteriorly (Gao & Fox 1991). Therefore, the specimen NMC 8891 is not a jaw of *Chamops segnis*, and a restudy of the specimen is needed.

Waldman (1970) described a lower jaw ramus (NMC 13563) from the Oldman Formation of southern Alberta, and referred to it as "*Chamops* sp.". Estes (1983a) subsequently referred the specimen to *Chamops segnis*, and reconstructed the mandible of *C. segnis* based on this specimen (Estes 1983a, fig. 22). But a recent restudy of this specimen resulted in its removal from *Chamops*, and referral to *Sphenosiagon* (Gao & Fox 1991). The specimen NMC 13563 shows a lightly built and wedge-shaped dentary, narrow subdental shelf, and poorly defined sulcus dentalis. All these are diagnostic features for *Sphenosiagon*, differing from those of *Chamops* and other teiids. The tooth crowns of NMC 13563 are partly dissolved, showing no cusp pattern, but another specimen (UALVP 29742) clearly shows that the tooth crowns of this lizard are unicuspid, rather than tricuspid, as in *Chamops*. For further discussion of *Sphenosiagon*, see below.

Sahni (1972) referred three specimens (AMNH 8486-8488) from the Judith River Formation, Montana to *Chamops segnis*, thereby extending the geologic record of this particular species from Lancian to Judithian. However, Sahni's (1972, fig. 8A-D) photographs show that AMNH 8486 and 8488 are too poorly preserved to show the diagnostic features of Lancian *Chamops segnis*, while AMNH 8487 is not figured but briefly mentioned in the description. AMNH 8486 (Sahni 1972, fig. 8A-B) is a robust dentary having only tooth bases preserved. The specimen shows no indication of having short-crowned, broadly tricuspid, and weakly heterodont teeth, which are characteristic for the Lancian *Chamops segnis*. Another specimen, AMNH 8488 (Sahni 1972, fig. 8C-D), is a maxillary fragment preserving four anterior teeth. Once again, the specimen shows none of the diagnostic characters for *Chamops segnis*: the short, slightly recurved, and unicuspid anterior maxillary teeth on this specimen are common in other teiids of the same age. From the above, there is no valid basis for identifying the two Judith River specimens (AMNH 8486, 8488) as the Lancian species *Chamops segnis*. It seems to be more appropriate to refer these specimens as "Teiidae gen. et sp. indet.". If the boat-shaped dentary configuration of AMNH 8486 can be broadly regarded as a significant similarity to *Chamops*, the specimen can be identified in no further detail than "?*Chamops* sp.".

Armstrong-Ziegler (1978, 1980) reported two teiids from the Fruitland Formation, New Mexico. She (1980) referred six specimens (UALP 75137D-E, 75137K-N) to *Leptochamops denticulatus*, and one specimen (MNA Pl. 1613) to *Chamops segnis*. These seem to be the first teiids known from the Fruitland Formation. But this study shows that the above referrals are either in error or unconvincing: all the specimens referred to *Leptochamops denticulatus* are misidentified (see discussion of *Leptochamops* below). The specimen MNA Pl. 1613 is a dentary fragment having one tooth and the base of another. The specimen is too fragmentary to be identified as *Chamops segnis* or even *Chamops*. The specimen can be more appropriately referred as to "Teiidae gen. et sp. indet.": it shows the subpleurodont dentition that is indicative of the family Teiidae, but shows no diagnostic features at either generic or specific levels.

Sullivan (1981) identified another specimen (UNM FKK-038a) from the Fruitland Formation as "cf. *Chamops segnis*", and stated that "this specimen, although somewhat larger than previously described specimens (Estes, 1964), agrees in every respect with the species *Chamops segnis*, where heterodonty is little pronounced and tooth crowns are not swollen" (Sullivan 1981: 77). The specimen is originally described as having "posteriad teeth [that] are tricuspid; anteriad teeth [that] are pointed and slightly recurved" (Sullivan 1981: 77). Probably based on this description, Estes (1983a) referred this specimen to *Chamops segnis*. However, the above mentioned statement and description are not in agreement with the illustrations of the original specimen (see Sullivan 1981, text-fig. 4.1). The drawings show that the anterior teeth on the specimen are either partially dissolved or broken, and the posterior teeth show no indication of having tricuspid crowns. From the illustrations, no evidence is available to show affinities with *Chamops segnis*, but the extremely heavy basal deposit of cementum around the tooth bases and the large replacement pits show some resemblance to some Tertiary tupinambines (e.g., *Tupinambis huilensis* and *Dracaena colombiana*, see Estes 1983a, fig. 23). There is no doubt that UNM FKK-038a represents a teiid, but its referral to *Chamops segnis* is questionable. When more specimens from the same formation become available, this specimen should be restudied.

Chamops sp.?

Plate 2, Figs. 6-10

Referred specimens: UALVP 29816-29818, 29820, 29826 (total: 5), maxillaries; UALVP 29819, dentary.

Locality and horizon: MR-6 locality, Verdigris Coulee, approximately 30 km east of the village of Milk River, southern Alberta; upper member of the Milk River Formation (Aquilan), Upper Cretaceous.

Description: The specimens UALVP 29816 and 29826 are both the posterior part of left maxillaries, each having five teeth preserved. The maxillary teeth are short, stout, and tricuspid. Although swollen in lateral view, the tooth bases are slightly compressed anteroposteriorly. These teeth are evidently subpleurodont, being attached to a low lateral parapet for about one-third of the tooth height. Dorsal and medial to the tooth row is a well-developed supradental shelf, which is separated from the tooth bases by a shallow but well defined sulcus dentalis (dental gutter).

The third fragmentary maxillary (UALVP 29817) has the posteriormost six teeth preserved. The specimen shows the same tooth form as that of the two maxillaries described above, but has two replacement pits developed at the bases of the last and the fourth most posterior teeth. The posterior interior alveolar foramen, as in the Lancian species Chamops segnis, opens above the fifth tooth position from the back.

Another maxillary, UALVP 29818, shows a short external premaxillary process and the more or less plate-like base for the medial process. A notch between the two processes is clearly recognizable on the specimen. The dorsal process (nasal process) of the bone rises abruptly behind the notch for the naris, forming a steep lateral wall of the maxillary.

Although dorsal and posteriorly broken, the preserved part shows that the dorsal process of this species is higher and more anteriorly steep than that of the Lancian Chamops segnis (see Estes 1964, fig. 47). The maxillary fragment shows the anteriormost five tooth positions (four teeth and the broken base of another). The teeth are conical but have swollen bases, and the tips of the crowns are slightly recurved.

The tooth form of this species is better shown on the specimens UALVP 29819 (dentary fragment) and UALVP 29820 (maxillary fragment). The former is a fragmentary right dentary having three teeth and the latter a left maxillary fragment bearing four teeth. The teeth are short and subpleurodont, and the tooth shafts are swollen, having a heavy deposit of cementum at the tooth bases. Having a "bottle neck" constriction, the crowns are slightly narrower than the swollen shafts, and in the middle and posterior part of the tooth row are broadly tricuspid. The main cusp is much stronger than the side cusps, and the anterior side cusp is in most cases more prominent than the posterior one. The unworn teeth on UALVP 29819 show that the crown surface has faint wrinkling or striations, which are more clearly shown lingually than labially.

Discussion: The six specimens described above represent the geologically oldest record of the genus Chamops, as the specimens were collected from the Milk River Formation (upper member), which is Aquilan age (L. S. Russell 1964, 1975; Fox 1976; Lillegraven & McKenna 1986; Lillegraven 1991), some 18 Myr earlier than Lancian (Harland et al. 1990).

The tooth form of these early Chamops teiids generally resembles that of Chamops segnis, but differs from the latter in having less swollen tooth shafts and less conspicuous side cusps compared to the main cusp (the three cusps in Lancian Chamops segnis are more nearly equally developed than in the Milk River form). The vertically directed anterior edge and the height of the nasal process (shown in UALVP 29818) differ from that of Chamops segnis (see Estes 1964, fig. 47). These differences on the maxillary structure and tooth form, enhanced by a 18 Myr chronological gap, indicate that the Milk River materials may represent a species different from Chamops segnis. However, the Aquilan specimens are too incomplete to confirm this possibility, and are best identified as "Chamops sp.?".

Genus *Socognathus* Gao & Fox 1991

Type species: *Socognathus unicupis* Gao & Fox 1991.

Range: Upper Cretaceous, North America.

Diagnosis: As for the type and only known species.

Socognathus unicuspis Gao & Fox 1991

Plate 3, Figs. 1-8; Text-fig. 7

Holotype: UALVP 29739, an incomplete left dentary having 11 well-preserved teeth and the bases of six others.

Type locality and horizon: Railway Grade locality, in Sec. 22, Tp. 20, R 12, W 4, southeastern Alberta; Upper Cretaceous Oldman Formation (Judithian in age).

Referred specimens: UALVP 29910-29911, incomplete tooth-bearing maxillaries from the Irvine locality; UALVP 29736, 29740, 29743-29745, and RTMP 82.24.57, incomplete tooth-bearing dentaries from the Irvine locality.

Known distribution: Upper Cretaceous Oldman Formation (Judithian in age), southeastern Alberta, Canada. Possible occurrence of the genus in the Hell Creek Formation is indicated by an unnumbered jaw fragment from the BCA locality, but cannot be confirmed owing to the poor preservation of the specimen.

Diagnosis: A large teiid differing from other teiids in the following combination of character states: dentary greatly elongated and robust; mandibular symphysis strongly enhanced by ventral bony buttress; dentary teeth mostly large, but variable in spacing and recurvature of crowns; tooth attachment subpleurodont, with lateral parapet low, about one-third of tooth height; tooth crowns unicuspid, but having moderately strong anterior ridge and weaker posterior ridge curving ventrolingually from apical cusp.

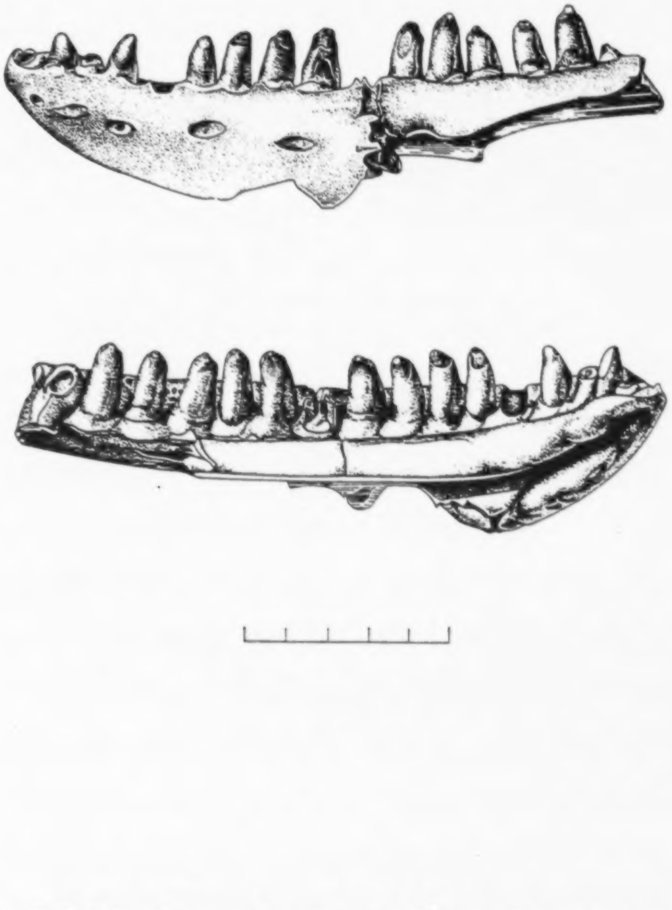
Description: The holotype (UALVP 29739) is a left dentary having 11 complete teeth and the bases of six others, with probably the last one or two teeth missing on account of breakage. The dentary is elongated but robust, and is straight when viewed from above. Medially, the dentary bears a sturdy subdental shelf, the dorsal (subdental) ridge of which borders a well-developed sulcus dentalis along the medial side of the tooth row. The shelf is relatively straight, gently narrowing posteriorly, with the anterior end turning slightly dorsomedially. The ventral side of the shelf bears a narrow but clearly defined groove for the dorsal splenodentary articulation, which terminates anteriorly below the sixth tooth positions, and extends posteriorly to the end of the dental shelf. Posteriorly, the inferior alveolar canal opens into the Meckelian canal through the posterior interior alveolar foramen below the thirteenth tooth position. The widely open Meckelian canal on the specimen indicates a significant hypertrophy of the splenial.

The dentary teeth are basically unicuspid, with no tendency towards developing tricuspid crowns, although the posterior teeth have stronger anterior and weaker posterior ridges curving ventrolingually. The tooth crowns are generally bent lingually but variably so; the teeth also vary in size, and spacing posteriorly along the tooth row (best shown on UALVP 29736). The tooth bases are slightly expanded laterally; a deposit of cement is clearly shown around the bases. The lateral parapet of the jaw is low, about one-third of the tooth height, and the dentary teeth are subpleurodont in the mode of their attachment. The holotype shows a suppression of tooth replacement (it is from a large, evidently mature, individual), but absorption pits can be seen on smaller specimens (e.g., UALVP 29740). The tooth row of the holotype is straight, but variation of this character is seen in UALVP 29736, which shows a strong curvature as in Leptochamops and Meniscognathus Estes 1964. The number of teeth anterior to the posterior interior alveolar foramen is about 13, posterior to the foramen five or six; therefore, the complete tooth row is estimated to include 18 to 20 teeth. The posterior teeth are obviously enlarged, resulting in a weakly developed heterodonty along the tooth row.

The external surface of the dentary is strongly convex dorsoventrally, and strongly swollen laterally as a consequence of the posterior expansion of the Meckelian canal. On the holotype, the inferior alveolar foramina on this surface increase posteriorly in size, and the spaces between the foramina lengthen as well, but these attributes seem to be somewhat irregular on other specimens, such as UALVP 29736. The lower and posterior part of the holotype, as in most other specimens, is missing as a consequence of breakage; however, the well-preserved anterior part suggests that the lower jaw is deeper than that of Leptochamops, but obviously shorter and shallower than that of the contemporaneous large teiid Glyptogenys Gao & Fox 1991.

UALVP 29910 is an incomplete left maxillary bearing nine teeth and the bases of three others. The specimen is smaller than the holotype dentary, indicating that it is from a younger individual. The maxillary is broken above the superior alveolar foramina and behind the twelveth tooth position, with the anterior end nearly complete. Medially, the specimen bears a strong supradental shelf, which medially borders a well-developed sulcus dentalis. The posterior interior alveolar foramen is located above the twelveth position in the maxillary tooth row (the last tooth remaining in the specimen). The first three teeth on the specimen are broken off, with only the bases preserved, but the remaining teeth are complete, except for the two in the middle of the tooth row, which have the apex of the crown broken off. As in the dentary specimens, the maxillary teeth are unicuspid, subpleurodont, and variable in size, spacing, and curvature along the tooth row. In lateral view, UALVP 29910 has a very short premaxillary process, and the facial process behind it rises abruptly, as in Chamops. The superior alveolar foramina laterally above the tooth row are small and are more or less equally spaced from one another. The lateral surface of the maxillary is unornamented but has numerous tiny foramina opening posterodorsally.

The other maxillary specimen in the collection (UALVP 29911) is a right maxillary fragment with seven teeth and the broken bases of nine others. The specimen is larger and more robust than UALVP 29910, and shows a nearly complete tooth count of the maxillary tooth row. The first tooth is broken, followed by seven complete teeth, and the remaining tooth bases of nine others. The posteriorly narrowed dental groove indicates that the maxillary tooth row is nearly complete, with probably one, at most two, positions missing; therefore, the maxillary probably had 17-18 tooth positions. The well-preserved teeth on this specimen show the same crown pattern and tooth attachment as the maxillary (UALVP 29910) and the dentaries described above, but shows a "step" of the tooth row at the sixth through the eighth positions, where the teeth are smaller and obviously younger than those anterior to them. This kind of "step" has been recognized from Chamops (see Estes 1964) and other lizards (see discussion on Chamops above). Unlike UALVP 29910, the ventral view of this specimen shows that the maxillary tooth row is strongly curved, corresponding to the facial constriction (narrowing) in front of the orbits. As in UALVP 29910, the posterior interior alveolar foramen is also open above the supradental shelf, at the level of the 12th tooth position. Posterior to the foramen and above the posteriormost four or five teeth, the supradental shelf bears a well developed groove along the lateral border of the maxillary. This groove is a clear indication of a tongue and groove articulation of the maxillary with the anterior ventral process of the jugal, which is unknown.



Text-fig. 7. Teiidae, Socognathus unicuspis, Oldman Formation, southeastern Alberta; UALVP 29739 (holotype), incomplete left dentary; (above) lateral view, (below) medial view. Scale = 5 mm.

Discussion: The referral of *Socognathus* to the Teiidae is mainly based on two character states: hypertrophy of the splenial (as indicated by the widely open Meckelian canal), and a heavy basal deposit of cementum; both are recognized synapomorphies of the family Teiidae (MacLean 1974; Presch 1974b; Estes 1983a; Estes et al. 1988). Some other character states, such as strong subdental shelf and well-developed sulcus dentalis, are also indicative of the Teiidae.

Socognathus unicuspis is now based on several well-preserved, tooth-bearing dentaries and maxillaries, as enumerated above. In addition, several uncatalogued fragmentary specimens from both the Railway Grade and Irvine localities are also referrable to this species. A comparison of the holotype dentary with the referred specimens allows reconstruction of the dentary proportions of this lizard, and shows that *Socognathus* differs in both tooth form and structure of the dentary from other teiids of the same age, including *Glyptogenys*, *Sphenosiagon*, and *Gerontoseps* Gao & Fox 1991, known from the same formation. A strong mandibular symphysis enhanced by a ventral bony buttress seems to be unique for *Socognathus unicuspis*, and hence offers no information about its relationship to other teiids. However, the large size of this lizard, variable spacing of the marginal teeth, and the tendency of the teeth to increase size posteriorly (resulting in a certain degree of heterodonty) are unique resemblances to Recent *Tupinambis*, a large omnivorous teiid distributed in tropical South America. Therefore, this Judithian teiid is probably referrable to the subfamily Tupinambinae (sensu Presch 1983), which includes the Recent genera *Tupinambis*, *Callopistes*, *Crocodilurus*, *Dracaena*, and the Late Cretaceous fossil genus *Chamops* (Estes 1964, 1983a; Presch 1983). Many large specimens of *Socognathus* show no absorption pits, indicating suppression of tooth replacement in adults, which has also been recognized in *Tupinambis* (MacLean 1974).

UALVP 29743 and 29744 from the Irvine locality are two small dentaries referred to *Socognathus unicuspis* with some uncertainty. The two specimens show a similar tooth form (cusp pattern) to the holotype, but the dentaries are slightly more slender, the anterior teeth are closely packed together, and the ventral bony buttress is weaker independent of size, compared to the holotype and referred specimens. Furthermore, UALVP 29743 and 29744 show that the subdental shelf sharply decreases in thickness posteriorly, differing from other specimens mentioned above. These two dentaries are tentatively referred to Socognathus unicuspis, awaiting further study on more and better preserved specimens to clarify their taxonomic position.

Genus Sphenosiagon Gao & Fox 1991

Type species: Sphenosiagon simplex Gao & Fox 1991.

Range: Upper Cretaceous, North America.

Diagnosis: As for the type and only known species.

Sphenosiagon simplex Gao & Fox 1991

Plate 4, Figs. 1-4; Text-fig. 8

1970 Chamops sp. Waldman, p. 546, figs. 2-3.

Holotype: UALVP 29742, incomplete left mandible having the splenial firmly articulated with the dentary, and having eight posterior teeth and the base of another.

Type locality and horizon: Outcrop of the Oldman Formation near Irvine, in Sec. 31, Tp. 11, R 2, W 4, about 40 km east of Medicine Hat, southeastern Alberta; Upper Cretaceous Oldman Formation (Judithian in age).

Referred specimen: NMC 13563, a tooth-bearing right mandibular ramus collected by C. M. Sternberg from Steveville, Alberta (Waldman 1970); UALVP 29732, topotypic dentary fragment; UALVP 29912, topotypic tooth-bearing maxillary. UALVP 29836-29837, fragmentary tooth-bearing dentaries from UALVP-MR-6 locality of the Milk River Formation.

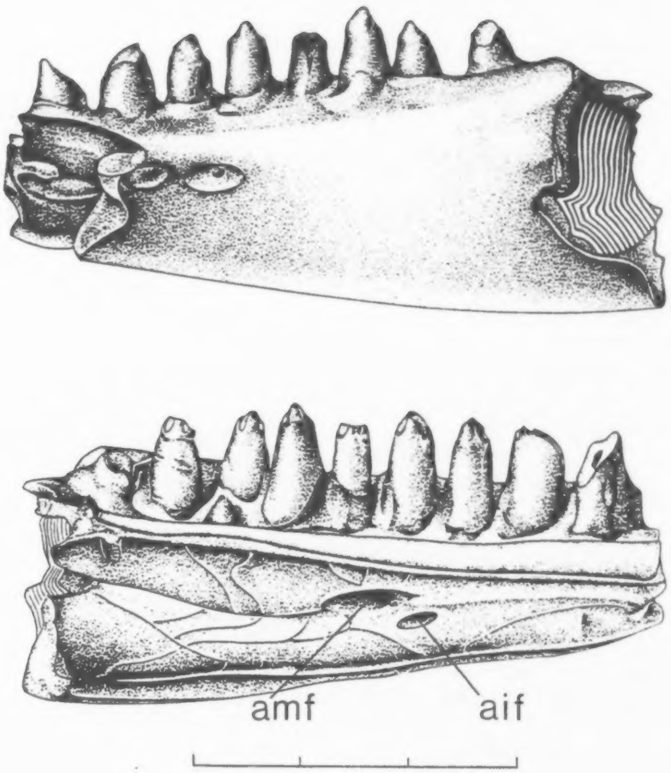
Known distribution: Upper Cretaceous Oldman Formation (Judithian in age), and the upper member of the Milk River Formation (Aquilan), southern Alberta, Canada.

Diagnosis: Differing from other Late Cretaceous teiids, including Leptochamops denticulatus, in having a combination of the following character states: dentary slender, lightly built, and wedge-shaped; subdental shelf narrow, with maximum depth less than half of tooth height; sulcus dentalis poorly defined; straight, pillar-like widely spaced teeth with pointed, unicuspid crowns; thickened tooth bases having heavy basal deposit of cementum; marginal teeth tending to be subacrodont, with lateral parapet less than half of tooth height.

Description: The holotype (UALVP 29742) consists of an incomplete tooth-bearing left dentary with firmly articulated splenial. The mandibular symphysis and the postdentary part of the jaw are missing. Sharply tapering anteriorly, the specimen clearly shows that the lower jaw of this lizard was wedge-shaped, lacking the boat-shaped curvature along the ventral border that is commonly seen in other teiids (e.g., Chamops, and Leptochamops). As shown as well on the referred specimens, the mandible is laterally compressed, so that its lateral surface is almost flat, differing from Socognathus and other contemporaneous teiids that also have a robust dentary. The small inferior alveolar foramina are unevenly spaced, and the posteriormost foramen is located anterior to the midpoint of the tooth row. The same arrangment of these foramina is also shown on NMC 13563, a right mandibular ramus that preserves a more nearly complete configuration of the jaw.

The medial surface of the jaw is concave, and is largely occupied by the hypertrophied and wedge-shaped splenial. Two Meckelian foramina (anterior inferior alveolar foramen and anterior mylohyoid foramen) are close to each other and penetrate the splenial to open into the Meckelian canal close to the midpoint of the tooth row. The splenial is firmly attached, but not fused, to the dentary, having clearly recognizable dorsal and ventral splenodentary sutures. The ventral suture is developed along the ventral edge of the jaw, not crossing laterally beyond the ventral mid-line. The slender subdental shelf is distinctive: the anterior maximum depth of the shelf is no more than half of the dentary tooth height, and is greatly diminished posteriorly. The dorsal ridge of the subdental shelf is so poorly-developed and so close to the tooth row that a sulcus dentalis is barely recognizable.

The holotype has eight posterior teeth and the base of another preserved. A comparison with NMC 13563 (referred specimen with a complete posterior end of the tooth row) suggests that the holotype may have the last one or two teeth missing (the latter specimen also has the anterior end broken off). Among the preserved teeth, three are complete, and the remaining ones have the crowns partly broken. The crowns are unicuspid with a pointed cusp forming an apex and a faint ridge on both mesial and distal side of the cusp. The tooth shafts are straight and are slightly thickened toward the tooth bases, giving a pillar-like configuration. An extensive, heavy basal deposit of cementum is clearly visible on the holotype and referred specimens. The dentary teeth are moderately spaced, forming a straight tooth row. The attachment of these teeth can be called subpleurodont, but the lateral parapet is so low (varying from slightly less than half to no more than one-third of the tooth height) and the dental gutter is so poorly defined, that the term subacrodont is almost as appropriate. One of the tooth positions (the fourth or fifth) on the holotype shows a tiny new tooth erupting posteromedial to the base of the tooth to be replaced. The replaced tooth, still on the functional tooth row, has been slightly pushed away laterally from the midline of the tooth row, showing a kind of irregular replacement compared to the "standard" teiid replacement pattern, with replacement teeth developing posteromedially, in subcircular replacement pits (Romer 1956).



Text-fig. 8. Teiidae, Sphenosiagon simplex, Oldman Formation, southeastern Alberta; UALVP 29742 (holotype), incomplete left mandible; (above) lateral view, (below) medial view. Scale = 3 mm. Abbreviations as in Text-fig. 2.

In the UALVP collections, two specimens (UALVP 29836-29837) from the upper member of the Milk River Formation document the Aquilan occurrence of Sphenosiagon simplex. One of the two (UALVP 29836, see Plate 4, Fig. 3) is the posterior part of a right dentary, with five complete teeth and the broken base for another. The dentary is larger than the holotype, but clearly resembles the latter in tooth form, spacing, and the mode of tooth attachment. The splenial is missing, leaving the Meckelian canal widely open, showing that a large posterior interior alveolar foramen opens under approximately the fourth most posterior tooth position.

The other specimen from the Milk River Formation (UALVP 29837) is the dentary fragment of an old individual, as evidenced from its size and robustness, and evident suppression of tooth replacement. Although fragmentary, this specimen is clearly referrable to Sphenosiagon simplex on its characteristic crown pattern and a distinct groove below the subdental shelf for the splenodentary articulation (Plate 4, Fig. 4).

Discussion: The lizard Sphenosiagon simplex from the Oldman and Milk River formations clearly shows a large splenial covering almost the entire medial side of the dentary and a heavy basal deposit of cementum around the tooth bases; therefore, the lizard is referrable to the family Teiidae.

1) Taxonomic Assignment of NMC 13563

Waldman (1970) described a right mandible (NMC 13563) from the Oldman Formation, southeastern Alberta, which he identified as Chamops sp.; this specimen was subsequently referred to Chamops segnis by Estes (1983a: 95). A reconstruction of the mandible of Chamops segnis given by Estes (1983a: 94) is also based on NMC 13563. However, restudy of this specimen strongly indicates that the NMC 13563 does not belong to Chamops segnis and should be allocated to Sphenosiagon simplex, as Gao & Fox (1991) demonstrated.

First, a comparison of NMC 13563 with UALVP 29742 (holotype of Sphenosiagon simplex) shows that the two specimens belong to the same species: they show the same unique jaw shape, the same development of the splenial that is firmly attached to the dentary, a much more narrow subdental shelf than in Chamops segnis, a poorly defined sulcus dentalis, and the same kind of tooth attachment. Second, although the tooth crowns on NMC 13563 have been partially dissolved diagenetically, those on the holotype (UALVP 29742) are unambiguously unicuspid, not tricuspid as in Chamops segnis, nor do the crowns display the barrel-like proportions that Estes (1983a, fig. 22) illustrated for NMC 13563; in fact, Estes' figure differs substantially from that of Waldman (1970, fig. 2), which is the more accurate, and has been drawn so that it appears to be more Chamops-like than it is. For example, no "surangular window" is preserved on NMC 13563 (see Estes 1983a: 94), and the so-called "coronoid" which both Waldman (1970) and Estes (1983a) have shown, is actually a piece of unidentifiable postdentary bone glued into the position of a coronoid. Therefore, future restudy of the specimen may well change the reconstruction of the jaw.

Waldman (1970) estimated that the full tooth count of NMC 13563 is about 15, which is correct. He wrote that the "dental gutters are present on both sides of the tooth-row" (Waldman 1970: 546) on NMC 13563, which is unlikely for any lizard taxon. In fact, on NMC 13563, only the eighth tooth from the back is located more medially than the others, leaving a short space from the low lateral parapet of the dentary. This tooth is not fully functional, but is still developing and is not yet attached to the lateral parapet of the jaw. All the remaining teeth are tightly attached to the low lateral parapet, and there is no dental gutter along the labial side of the tooth row.

2) Comments on Several Characters of Sphenosiagon simplex

The Judithian teiid Sphenosiagon simplex clearly shows several osteological characters that are worth special notice. One, and probably the most important, of these characters is the tendency towards subacrodonty. The tooth attachment in teiids can be either subpleurodont, as in modern Kentropyx Spix 1825 and in fossil Leptochamops, or subacrodont, as in modern Teius Merrem 1820 and fossil Haptosphenus. The Judithian species Sphenosiagon simplex demonstrates a tendency towards a subacrodont tooth attachment: the dental gutter is so poorly developed, and the lateral parapet of the tooth row is so low, that the term subacrodont is almost appropriate. There is no true acrodont tooth attachment known in the family Teiidae; however, a subacrodont pattern has independently evolved in all three subgroups of the family (Polyglyphanodontinae, Teiinae, and Tupinambinae; sensu Presch 1983) as a more derived condition than subpleurodonty. The subacrodont condition is known from fossil forms such as the Campanian Adamisaurus Sulimski 1972, and the Maestrichtian Haptosphenus, Polyglyphanodon Gilmore 1940 (probably including Paraglyphanodon Gilmore 1940), and Peneteius Estes 1969a; all but the last genus are placed in the Polyglyphanodontinae (sensu Estes 1983a). According to Estes (1969a), Peneteius is close to Recent Teius. For Recent forms, at least the dentition of Teius, Dicrodon Dumeril & Bibron 1839, and Dracaena can be termed subacrodont. As far as is known among Late Cretaceous teiids, Adamisaurus and Haptosphenus demonstrate the most derived condition of subacrodonty in the family Teiidae.

Another character worth noting is the articulation of the splenial with the dentary. Unlike most fossil teiids, in which the splenial is often lost before burial, two specimens (holotype and NMC 13563) of Sphenosiagon have the splenial firmly attached to the dentary, even though the lower jaw is lightly built. A strong interlocking articulation between the splenial and the dentary may play a key role in the retention of the splenial. Two more fragmentary specimens (UALVP 29732, 29837) show that a deep groove is developed posteriorly on the ventral side of the subdental shelf, forming a strong interlocking articulation with the splenial. Differing from that of other teiids, this groove has a ventromedial tongue-like structure that prevents the splenial from sliding ventrally. It could be that this type of articulation has prevented the loss of the splenial in Sphenosiagon simplex. The functional meaning of this structure is unclear, but might be related to the feeding habit of this lizard, coupled with the nearly subacrodont dentition.

It is possible that preservation of the relatively fragile dentary with the splenial in articulation reflects only a taphonomic factor: the Irvine locality, from where the holotype of Sphenosiagon simplex was obtained, may represent an "in-channel locality" (Brinkman 1990), one containing a locally derived concentration of microfossils (Eberth 1990b). However, Waldman (1970: 542) thought that NMC 13563 had formed "part of the faeces of a crocodile of the genus Leidyosuchus", as he stated that the specimen was found "between the first sacral rib and the anterior margin of the left ischium, [and] together with the curiously eroded teeth, is, to me, highly suggestive of digested material" (Waldman 1970: 546). If NMC 13563 is indeed coprolitic in origin, the holotype (UALVP 29742) certainly represents splenial preservation under quite different conditions, because no "digestive erosion" is shown on the specimen. The two specimens from the upper member of the Milk River Formation are fragmentary and do not retain the splenial. This type of preservation may reflect the fact that the MR-6 locality represents a paleofacies that is slightly different from the Irvine locality.

Genus Glyptogenys Gao & Fox 1991

Type species: Glyptogenys ornata Gao & Fox 1991.

Range: Upper Cretaceous, North America.

Diagnosis: As for the type and only known species.

Glyptogenys ornata Gao & Fox 1991

Plate 4, Figs. 5-8; Text-fig. 9

Holotype: UALVP 29735, incomplete left dentary bearing 12 well-preserved teeth and spaces for two others.

Type locality and horizon: Outcrop of the Oldman Formation near Irvine, in Sec. 31, Tp. 11, R 2, W 4, about 40 km east of Medicine Hat, southeastern Alberta; Upper Cretaceous Oldman Formation (Judithian in age).

Referred speciemens: UALVP 2036, 29756, 29758-29759, 29913, 29767, 29769, all tooth-bearing dentaries, and all topotypic but 29758 from the Railway Grade locality of the same formation. Several unnumbered jaw fragments from both Irvine and the Railway Grade localities are also referrable to this species.

Known distribution: Upper Cretaceous Oldman Formation (Judithian), southeastern Alberta, Canada. Several unnumbered dentary fragments indicate possible occurrence of this lizard in the Milk River Formation (Aquilan in age), but this cannot be confirmed, owing to the poor preservation of the specimens.

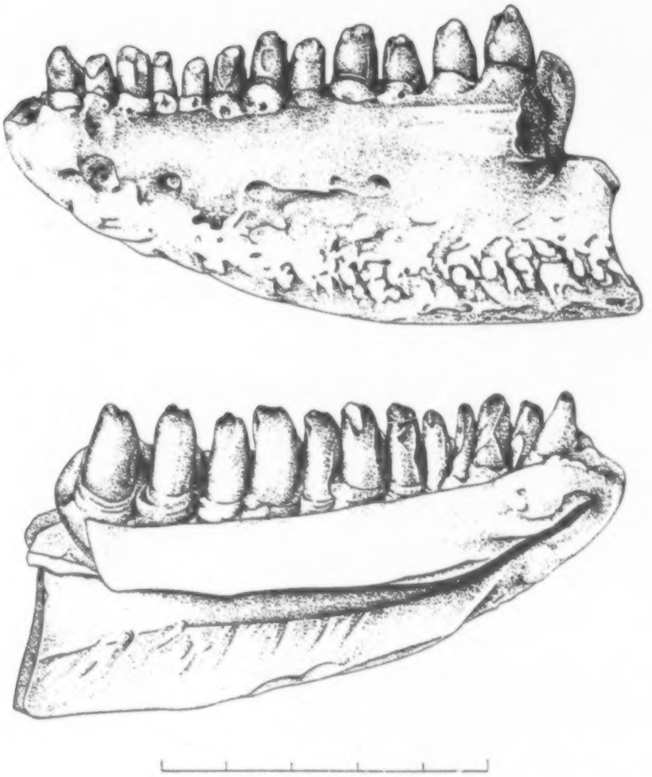
Diagnosis: A large teiid lizard differing from other Late Cretaceous and Recent teiids in having the following combination of character states: dentary deep, massively built, and at least in adult individuals, heavily ornamented below inferior alveolar foramina; subdental shelf deep and robust, maximum depth same as dentary tooth height; teeth subpleurodont, basically bicuspid with anterior ones bluntly conical; tooth bases compressed anteroposteriorly, having thick, ring-like basal deposit of cementum.

Description: The holotype (UALVP 29735) is an incomplete but well-preserved left dentary, broken immediately behind the 14th tooth position. The dentary is short, deep, massively built, and laterally compressed. It has a deep, boat-shaped curvature along the ventral border, but tapers anteriorly and terminates with an extremely weak mandibular symphysis in relation to the size of the jaw.

Medially, the dentary bears a deep and strong subdental shelf, the maximum depth of which is about the same height as the dentary teeth. The dorsal ridge of the shelf forms the medial border of a narrow and shallow sulcus dentalis along the lingual side of the tooth row. The ventromedial edge of the shelf bears a deep groove for the dorsal edge of a strong splenial. The anterior termination of this groove indicates that the splenial extended anteriorly to a point below the sixth anteriormost tooth position. The anterior end of the shelf bears a blunt but prominent dorsomedial process, forming part of the mandibular symphysis. Below the process is a short, fissure-like anterior Meckelian foramen developed under the first six tooth positions. Posteriorly below the deep and robust subdental shelf, the Meckelian sulcus is widely open, and no splenial is preserved; the Meckelian sulcus occupies over half of the total depth of the dentary. The lower border of the dentary is a sharp edge, which is posteriorly straight but anteriorly turns medially and upward to the mandibular symphysis. On the meidal side of the ventral border, a large surface area for the ventral splenodentary articulation is clearly visible on the specimen, indicating a strong splenodentary articulation along the ventromedial side of the jaw.

The dentary is laterally flattened, but weakly convex posteriorly. A row of small inferior alveolar foramina (external mental foramina) perforate its dorsal external surface, and the spaces between the foramina obviously increase in length posteriorly. These foramina are rounded and extremely small in relation to the size of the jaw. The external surface of the dentary is smooth above the foramina, but is heavily ornamented below, with irregular bony rugae. Other specimens show that the external ornamentation is variable in extent, ranging from the ventral edge of the jaw to dorsally above the line of mental foramina. Generally, larger individuals show more extensive ornamentation than smaller ones.

The preserved part of the holotype dentary bears 12 teeth and the bases of two to three others. The teeth are short, stout, closely spaced, and subpleurodont in their mode of attachment. The tooth bases are slightly compressed anteroposteriorly, having a ring of cement around the base of each tooth. The first five or six teeth are slightly procumbent, bluntly conical, more closely spaced, and more anteroposteriorly compressed than the posterior ones. The teeth posterior to the sixth are bicuspid, with a tiny accessary cusp developed anterior of the main cusp. The crowns of these posterior teeth are slightly tipped medioposteriorly, and the bases increasingly swollen posteriorly, although they are also laterally expanded. The tooth row is relatively straight, but the complete tooth count is unknown, with the teeth posterior to the 13th broken away.



Text-fig. 9. Teiidae, *Glyptogenys ornata*, Oldman Formation, southeastern Alberta; UALVP 29735 (holotype), incomplete left dentary; (above) lateral view, (below) medial view. Scale = 5 mm.

Discussion: The familial assignment of Glyptogenys ornata to the Teiidae is mainly based on the conspicuous basal deposit of cementum at the tooth bases, and the enlarged splenial, as indicated by the widely open Meckelian canal in the holotype. These are well-recognized synapomorphies of the family Teiidae (MacLean 1974; Presch 1974b; Estes 1983a; Estes et al. 1988). Another synapomorphy often recognizable on fragmentary dentaries is that the replacement teeth develop posteromedially within subcircular tooth cavities (Romer 1956; Estes et al. 1988). However, this character is not shown on the holotype specimen, obviously a result of suppression of tooth replacement in adult individuals.

The dentary tooth row on the holotype is incomplete, with probably the posterior five to seven teeth missing. It is possible when complete specimens are discovered that the most posterior teeth will prove to be tricuspid or incipiently tricuspid, as the combination of anterior conical with middle bicuspid and posterior tricuspid teeth is common in both living teiids (such as Crocodiluris lacertinus, Tupinambis nigropunctatus) and fossil species (such as Meniscognathus altmani).

One of the most obvious characters of the holotype is the sculptured lateral surface of the dentary. This sculpture is so pronounced that it is taxonomically significant. Osteodermal sculpture on the lower jaw is not common among modern teiids. At hand is a skull with mandibles of Cnemidophorus tigris (UMMZ 182042) that shows that the lower jaw is ornamented; however, the sculpture on this specimen is developed mostly on the angular bone and is much less heavy than that in Glyptogenys. A condition similar to C. tigris is seen in the Ameiva group (pers. observ.). There is no indication of lower jaw ornamentation being synapomorphic for any subgroup of the Teiidae; it seems that this character has been independently developed in Glyptogenys, and in Recent forms such as Ameiva and Cnemidophorus. The latter two genera are more closely related to each other than to any of the other genera of the family (Gorman 1970; Presch 1974a), while Glyptogenys shows no feature resembling the latter two genera in terms of jaw shape and tooth form: Ameiva and

Cnemidophorus have a slender mandible with pointed, bicuspid or tricuspid teeth, suitable for feeding on soft-shelled insects; while the deep and robust jaw with thick and bluntly bicuspid teeth in Glyptogenys are best designed for prey on hard-shelled beetles or other resistant terrestrial invertebrates.

The sculpture on the lower jaw may also be ontogenetically significant in some lizards. Etheridge (1964) showed ontogenetic development of sculpture on a series of dentaries in Anolis iguanids. However, it seems that Glyptogenys may represent a different case, because the holotype was probably not from an old individual (as evidenced by the unworn tooth crowns), but shows extensive ornamentation on the jaw nonetheless. In addition, two small jaw fragments (unnumbered specimens) in the UALVP collection show heavy sculpture, while a larger specimen (UALVP 29756) shows less heavy sculpture. Perhaps the ornamentation in this lizard is sexually dimorphic, but this interpretation is more problematic, because of the small sample size of the specimens for this lizard presently available; there is no evidence from modern lizards supporting this interpretation.

Genus Gerontoseps Gao & Fox 1991

Type species: Gerontoseps irvinensis Gao & Fox 1991.

Range: Upper Cretaceous, North America.

Diagnosis: As for the type and only known species.

Gerontoseps irvinensis Gao & Fox 1991

Plate 5, Figs. 1-4; Text-fig. 10

Holotype: UALVP 29754, an anterior part of a right mandible having 13 tooth positions.

Type locality and horizon: Outcrop of the Oldman Formation near Irvine, in Sec. 31, Tp. 11, R. 2, W. 4, about 40 km east of Medicine Hat, southeastern Alberta; Upper Cretaceous Oldman Formation (Judithian in age).

Referred specimens: UALVP 29757, 29760-29762, 29765-29766, 29768, all incomplete tooth-bearing dentaries. In addition, several unnumbered dentary fragments from the same horizon are also referrable to this species.

Known distribution: Upper Cretaceous Oldman Formation (Judithian); southeastern Alberta, Canada.

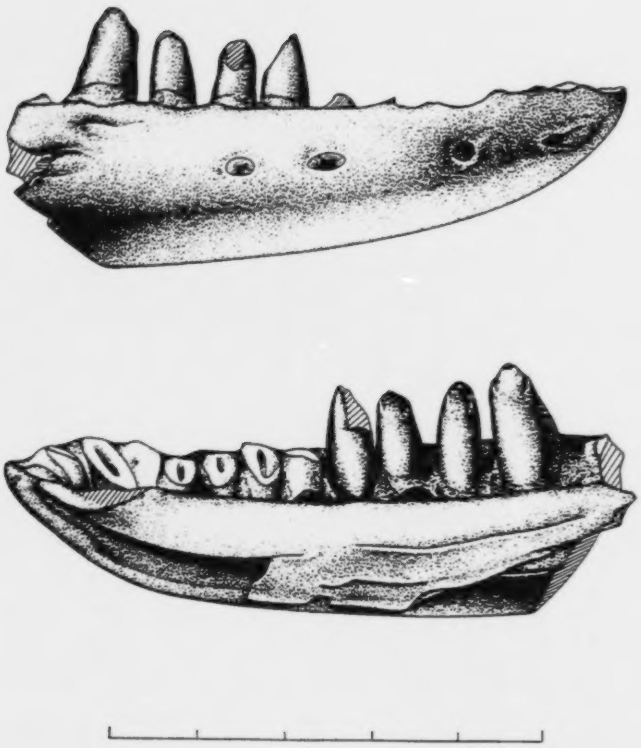
Diagnosis: Late Cretaceous teiid differing from other fossil and Recent forms of the same family in having the following combination of character states: mandible shallow but wide and strong, convex both laterally and medially; splenial partially fused to dentary; sulcus dentalis narrow and conspicuously deep; dentary teeth subpleurodont, with lateral parapet about one-third of tooth height; tooth crowns bluntly unicuspid, nearly conical, but having symmetrical anterior and posterior ridges; Meckelian canal an inverted triangle in cross section.

Description: The holotype (UALVP 29754) is an incomplete right mandible having the splenial partially fused to dentary. The jaw is relatively shallow, but strong and convex both lateral and medially. The lateral convexity is probably characteristic for this species, since the lateral surface is greatly swollen at a 45 degree angle below the line of the inferior alveolar foramina, making the lateral surface roughly ">-shaped" in cross-section. The medial surface has a similar but much weaker convexity. This particular type of convexity gives the Meckelian canal an inverted trianglar shape in cross-section.

In medial view, the subdental shelf is deep anteriorly but sharply reduced posteriorly. The shelf dorsally bears a sharp ridge (subdental ridge), which forms the medial border of a narrow and deep sulcus dentalis. Below the shelf, the splenial is deep posteriorly but greatly tapers anteriorly and terminates below the sixth or the seventh tooth from the front, leaving a narrow and elongated anterior opening for the Meckelian canal. The splenial is dorsally fused to the dentary, along the splenodentary suture, which is mostly still recognizable, but the suture is lost below the seventh and eighth teeth as well as posterior to the twelfth tooth position. The ventral splenodentary articulation remains unfused, and is located medially along the ventral border of the jaw. The Meckelian canal is restricted in comparison to that of Glyptogenys and Socognathus (see above), but has a wide and horizontal "roof" below the subdental shelf, causing the canal to be shaped as an inverted triangle in cross-section.

The holotype shows the anteriormost 13 tooth positions of the jaw, including four teeth (three complete) and the broken bases of nine others. The anterior six or seven teeth are slightly compressed anteroposteriorly, but the middle and posterior teeth are increasingly columnar, swollen, and widely spaced from one another. Tooth attachment is subpleurodont, with the lateral parapet as low as one-third of the tooth height. The tooth crowns are bluntly unicuspid, nearly conical, but have symmetrical anterior and posterior ridges. The basal deposit of cementum is less heavy than in Glyptogenys and Socognathus. Replacement pits are developed at the medial side of the base of the eighth and tenth teeth.

Among the referred specimens, UALVP 29760-29761 are better preserved than the others. These specimens clearly show the same kind of tooth form as the holotype, but the fusion between the splenial and dentary is not developed. Like the holotype, the two specimens have 13 or 14 dentary teeth preserved. These specimens are mostly broken at or in front of the posterior interior alveolar foramen. This gives an indication that the total tooth count of Gerontoseps is approximately 18 on the dentary, since the number of tooth positions posterior to the foramen is usually four to five in teiids.



Text-fig. 10. Teiidae, *Gerontoseps irvinensis*, Oldman Formation, southeastern Alberta; UALVP 29754 (holotype), incomplete right mandible; (above) lateral view, (below) medial view. Scale = 5 mm.

Discussion: One of the most obvious characters of the holotype (UALVP 29754) is the fusion of the splenial with the dentary along the dorsal splenodentary suture. Gao and Fox (1991) interpreted this fusion on UALVP 29754 as taxonomically significant, owing to the small size of the specimen and the low probability that such extensive fusion would occur in such a young individual. Now with more specimens in the collection, such as UALVP 29760-29761 described above, the fusion appears to be individually variable. The holotype probably represents a mature individual, in spite of its small size and unworn tooth crowns. This type of fusion is obviously different from the Meckelian canal enclosure in xantusiids, gymnophthalmids (MacLean 1974), some scincids (Greer 1970), iguanids (Etheridge & de Queiroz 1988), and amphisbaenians (Gans 1978), because the latter condition is associated with splenial reduction, while the splenial in Gerontoseps is large. The deep sulcus dentalis, well-defined subdental shelf, large splenial, and subpleurodont dentition are all consistent with classification of Gerontoseps in the Teiidae.

Splenodentary fusion is also known in the Lancian teiid Haptosphenus (Estes 1964), but Gerontoseps is substantially different from the latter in other aspects of jaw construction and tooth form (see Estes 1964, 1983a). The dentary teeth of Gerontoseps are basically conical. Although having symmetrical side ridges, the crown pattern of this lizard shows no tendency towards developing a tricuspid or incipiently tricuspid crown. Instead, the bluntly unicuspid teeth of Gerontoseps increase in size posteriorly, showing a tendency to develop molariform cheek teeth. These features combined with the shortness of the jaw, indicate a crushing function. Perhaps this lizard had a food preference for small hard-shelled insects.

Genus Leptochamops Estes 1964

Type species: Chamops denticulatus Gilmore 1928.

Included species: The species Leptochamops denticulatus Estes 1964, L. thrinax Gao & Fox 1991, and Leptochamops sp. (cf. L. denticulatus) are currently included in this genus.

Range: North American Upper Cretaceous Lance Formation, Hell Creek Formation, Frenchman Formation (all Lancian in age); and Oldman Foramtion (Judithian in age).

Diagnosis (revised from Estes 1964, 1983a): A Late Cretaceous teiid lizard resembling the modern Kentropyx-Cnemidophorus-Ameiva group in having a laterally concave dentary coupled with a curved dentary tooth row, but differing from the group in having the unique combination of the following character states: dentary slender and long, subdental shelf narrow and strongly dorsoventrally concave; marginal teeth high-crowned, subpleurodont, having cylindrical shaft and tricuspid crown.

Leptochamops denticulatus (Gilmore 1928) Estes 1964

Plate 5, Figs. 5-8

Referred specimens: Frenchman Formation, Gryde locality: SMNH P1927.231, P1927.871, P1927.908, P2004.89, fragmentary maxillaries; SMNH P1927.872, P1927.893, P2004.129, fragmentary dentaries.

Known distribution: Upper Cretaceous Lance Formation, eastern Wyoming; Hell Creek Formation, eastern Montana; Frenchman Formation, southwestern Saskatchewan (all Lancian in age).

Diagnosis (revised from Estes 1964, 1983a): A Late Cretaceous teiid differing from the closely related Meniscognathus Estes 1964 in having the following combination of character states: marginal teeth high-crowned, and weakly tricuspid; subdental shelf more slender and strongly dorsoventrally curved.

Description: The referred specimens from the Frenchman Formation include four maxillaries and two dentaries, all collected from the Gryde locality, Frenchman River Valley, southwestern Saskatchewan. Among these specimens, two (SMNH P1927.231, P1927.893) are better preserved than the others in terms of showing tooth morphology. SMNH P1927.231 (Pl. 5, Fig. 5) is the posterior part of a left maxillary, with six complete teeth and the base of another. Although fragmentary, the well-preserved teeth are characteristically of Leptochamops denticulatus type: cylindrical, high-crowned, and posteriorly tricuspid. Tooth attachment is subpleurodont, with more than one half of the tooth height projecting ventrally over the low lateral parapet of the maxillary. In medial view, the supradental shelf is much more slender than in Chamops segnis, but similar to that of Mensicognathus altmani from the same horizon. In ventral view, the posterior narrowing of the shelf indicates that the specimen is broken posteriorly close to the end of tooth row, with probably only one posteriormost tooth missing. The other specimen (SMNH P1927.893) consists of a fragmentary left dentary, having six posterior teeth preserved. The subdental shelf is slender, different from that in Chamops segnis and Meniscognathus altmani. This specimen is too fragmentary to show the dentary structure of this lizard, but the teeth preserved resemble those on SMNH P1927.231 in cusp pattern and the mode of attachment.

Discussion: Gilmore (1928) founded a new species, Chamops denticulatus, on several jaws from the Lance Formation. The holotype (YUM 1062), a complete left dentary containing 23 teeth, was the specimen originally assigned to Chamops segnis as one of the "dentary bones with precisely similar teeth, and corresponding in size with the jaws figured" (Marsh 1892: 450). Estes (1964) erected a new genus, Leptochamops, for Chamops denticulatus. The holotype that Estes cited as USNM 16514 is the same specimen as Gilmore's YUM 1062. The change of the specimen number was apparently a result of an exchange of specimens between Yale and the Smithsonian Institution in early 1920s (M. A. Turner pers. comm. 1989).

In the original description, Gilmore (1928) placed Chamops denticulatus in the Iguanidae. This familial assignment was largely based on Camp's (1923) comments on form and attachment of the teeth in Chamops segnis, which included the specimens of the then-unrecognized Chamops denticulatus. Estes (1964) revised Gilmore's Chamops denticulatus by referring it to the new genus Leptochamops, and he confirmed its relationship with teiids. More recently, Estes (1983a) pointed out the possible relationship of Leptochamops denticulatus with the living Kentropyx-Cnemidophorus-Ameiva group on the resemblance in the curvature of the tooth row.

The species Leptochamops denticulatus is only definitely known from the Lance, Hell Creek, and the Frenchman formations (all Lancian in age). Supposed pre-Lancian Leptochamops denticulatus has been reported from Montana and New Mexico, but these reports are unconvincing or simply based on misidentified specimens, as discussed below:

1) Sahni (1972) identified two specimens (AMNH 8490, 8491) as Leptochamops denticulatus and stated that "the Judith River material of Leptochamops denticulatus is identical to that from the Lance Formation" (Sahni 1972: 353). AMNH 8490 (fragmentary dentary) is not figured, while the maxillary fragment AMNH 8491 (Sahni 1972, fig. 8K) shows essentially conical rather than tricuspid or incipiently tricuspid crown pattern, and the anterior teeth are slightly recurved rather than procumbent. The maxillary structure of Leptochamops was previously not well known, but the newly collected UALVP 29746 from the BTB locality, Lance Formation, shows some significant features of this teiid. The

specimen consists of an incomplete right maxillary, having 14 tooth positions preserved (three complete teeth and spaces for 11 others). The maxillary anteriorly bears a premaxillary process, which is obviously longer and more slender than that of Chamops segnis from the same horizon, indicating a pointed snout in this teiid, similar to that of the Recent Cnemidophorus (see Presch 1970). The three teeth preserved on the maxillary clearly show the characteristic tooth form of L. denticulatus: high-crowned, cylindrical teeth with an incipiently tricuspid crown pattern. The seventh anterior tooth has developed a replacement pit, in which a small, newly erupting tooth can be seen. A large posterior interior alveolar foramen opens above the supradental shelf at the 13th tooth position. The concave lateral surface of the maxillary in combination with the elongated premaxillary process indicates a pointed snout in this lizard. AMNH 8491 lacks these features, and shows no significant resemblance to to Lancian Leptochamops denticulatus in terms of tooth form or jaw configuration. Therefore, AMNH 8491 would be better referred to "Teiidae gen. et sp. indet.," as it shows generally a teiid appearance, but lacks other features for detailed generic and specific identification.

2) Armstrong-Ziegler (1978), in a faunal list, reported the occurrence of Leptochamops denticulatus, together with Chamops segnis, from the Fruitland Formation, New Mexico. Subsequently, the same author (1980) in a descriptive paper referred six jaw fragments (UALP 75137D-E, K-N) to Leptochamops denticulatus; and this identification was accepted in Estes' (1983a) monographic review of fossil lizards. Unfortunately, from the description and the photographs, these fragmentary specimens appear to be taxonomically, and some are anatomically, misidentified, as well. "The most complete and diagnostic dentary in the collection at hand is specimen No. UALP 75137-K" (Armstrong-Ziegler 1980: 18). This "dentary" (possibly an incomplete maxillary, judging from the description) is not figured, but another "dentary" (UALP 75137D, plate 2d) is neither a dentary nor of a lizard. Instead, the enlarged photograph of UALP 75137D strongly indicates that it is the

premaxillary of *Albanerpeton*, an aberrant amphibian previously thought to be a prosirenid salamander (see Fox & Naylor 1982). The original description of UALP 75137K, "the most complete and diagnostic dentary" (Armstrong-Ziegler 1980: 18), stated that "many of the tooth crowns have a black shaft capped by a sharply contrasting light brown occlusal surface" (ibid.). This description and the photograph of UALP 75137D give a clear picture of the teeth of *Albanerpeton* rather than those of a lizard (see Fox & Naylor 1982).

Two other specimens (UALP 75137M-N), have "bicolored teeth that extend about one-half their height over the parapet of the deep dorsoventral border of the bone" (Armstrong-Ziegler 1980: 20); these are also referrable to *Albanerpeton*. The specimen 75137E was neither mentioned in the description nor figured in Armstrong-Ziegler's paper.

Consequently, the six specimens from the Fruitland Formation have been misidentified as *Leptochamops denticulatus*, and *Leptochamops* is not known from the formation, at least on the basis of currently available material. The identification of AMNH 8490-91 as *Leptochamops denticulatus* is unconvincing; hence, this species is also unknown from the Judith River Formation of Montana. Several specimens of pre-Lancian *Leptochamops* are known from the Oldman Formation, but can not be assigned to Lancian species *L. denticulatus* with certainty (see later discussion).

Leptochamops thrinax Gao & Fox 1991

Plate 6, Figs. 1-4; Text-fig. 11

Holotype: UALVP 29749, an incomplete left dentary bearing five teeth and bases of ten others.

Type locality and horizon: Outcrop of the Oldman Formation near Irvine, in Sec. 31, Tp. 11, R. 2, W. 4, about 40 km east of Medicine Hat, southeastern Alberta; Upper Cretaceous Oldman Formation (Judithian in age).

Referred specimens: UALVP 29748, 29750, 29753; all incomplete dentaries having several teeth preserved, and all collected from the Irvine locality.

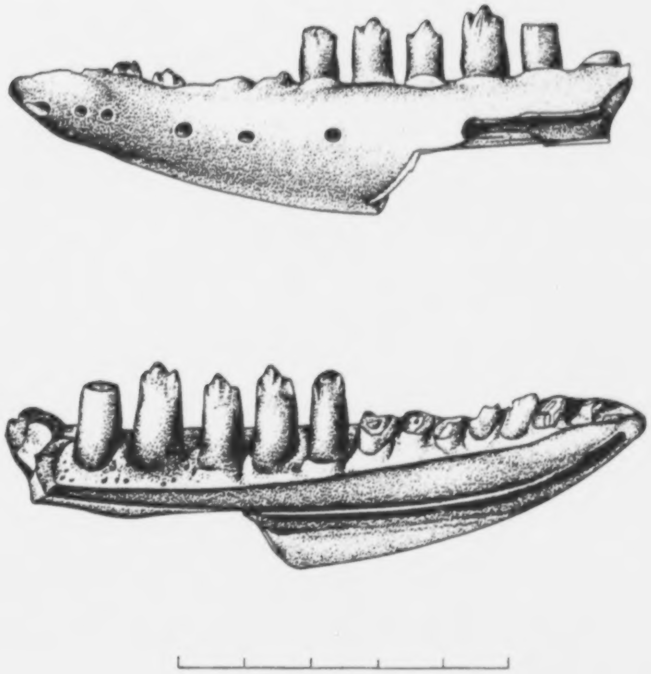
Known distribution: Upper Cretaceous Oldman Formation (Judithian); southeastern Alberta, Canada.

Diagnosis: A Judithian species of Leptochamops differing from the Lancian L. denticulatus in having the dentary teeth broadly tricuspid, widely spaced, and fewer in number; subdental shelf relatively straight and stronger; and Meckelian canal more restricted.

Description: The dentary (UALVP 29749) is long and slender, gently tapering anteriorly and having a pointed anterior end. It is relatively straight in dorsal view in comparison to that of Leptochamops denticulatus.

Medially, the dentary bears a well-developed subdental shelf, which abruptly diminishes in depth posteriorly, in contrast to the gentle reduction in depth seen in L. denticulatus. The subdental shelf is relatively straight by comparison, not curving dorsally at its anterior end. The dorsal ridge of the shelf is low, medially bordering a narrow and shallow sulcus dentalis along the tooth bases. The Meckelian canal takes up about half depth of the dentary, and thus, is more restricted than in L. denticulatus, indicating a more narrow splenial. The dorsal groove and the ventral surface for the splenodentary articulation show that the splenial terminates under the seventh anteriormost tooth position, leaving a long, narrow and fissure-like anterior Meckelian foramen.

Laterally, the external surface of the dentary is smooth, and is more convex posteriorly than anteriorly. Seven inferior alveolar foramina can be seen on the holotype, but other specimens, such as UALVP 29748 and 29753, show that the number and the arrangment of these foramina are individually variable. The holotype dentary bears five teeth and the bases of ten others. The dentary teeth are high-crowned, cylindrical, widely spaced, and subpleurodont in their mode of attachment. The tooth crowns, slightly tipped lingually, are broadly tricuspid, having a prominent central cusp and two much less prominant accessory cusps. The anterior cusp is stronger and more clearly separated from the main cusp than the tiny posterior accessory cusp. The complete tooth count for this species is estimated as 16 or 17, on the basis of the termination of the subdental shelf (the tooth row usually ends slightly anterior to where the subdental shelf meets the coronoid). In dorsal view, the tooth row is nearly straight, lacking the characteristic curvature seen in the Lancian species L. denticulatus and Meniscognathus altmani Estes 1964. The tooth bases are surrounded with a basal deposit of cementum, as commonly seen in other fossil teiids.



Text-fig. 11. Teiidae, *Leptochamops thrinax*, Oldman Formation, southeastern Alberta; UALVP 29749 (holotype), incomplete left dentary; (above) lateral view, (below) medial view. Scale = 5 mm.

Discussion: The holotype UALVP 29749 shows several taxonomically significant characters, including long and slender dentary, weak mandibular symphysis, restricted Meckelian canal, and straight, cylindrical, high-crowned teeth, that distinguish this lizard from other teiids from the Oldman Formation, including *Gerontoseps* and *Socognathus*. On the basis of these same features, Gao & Fox (1991) referred this lizard to *Leptochamops* Estes 1964, distinguishing it from the Lancian *L*. *denticulatus*. When compared to *L*. *denticulatus*, its nearly straight subdental shelf, strongly tricuspid and widely spaced dentary teeth, and nearly straight tooth row indicate differences at the specific level.

Several other specimens from the same formation show character states that more closely resemble *L*. *denticulatus* than *L*. *thrinax* (see later discussion), suggesting that the above mentioned differences may be generically significant. Indeed, if the polarity for the dentition of *Leptochamops* and the closely related *Kentropyx*-*Cnemidophorus*-*Ameiva* group is from incipiently tricuspid to fully tricuspid teeth, the Judithian *L*. *thrinax* with broadly tricuspid teeth may be less closely related to *L*. *denticulatus* than Gao & Fox (1991) thought. However, current understanding of *L*. *thrinax* is not yet sufficient to separate it from the Lancian *L*. *denticulatus* at generic level.

Leptochamops sp. (cf. L. denticulatus)

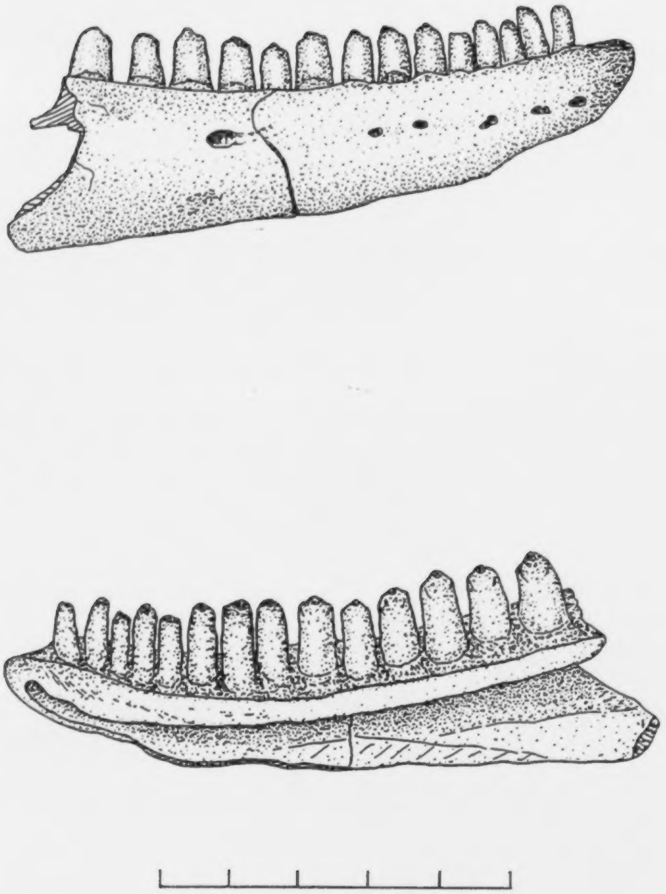
Plate 6, Figs. 5-6; Text-fig. 12

Referred specimens: UALVP 29741, 29772, right dentaries each having 16 tooth positions preserved.

Locality and horizon: Outcrop of the Upper Cretaceous Oldman Formation near Irvine, about 40 Km east of Medicine Hat, southeastern Alberta, Canada.

Description: The specimen UALVP 29772 is an almost complete right dentary having 14 complete teeth and the bases of two others. Medially, as in the Lancian Leptochamops denticulatus, the dentary bears a slender but well-defined subdental shelf. The shelf curves upwards anteriorly and gently diminishes posteriorly, differing from L. thrinax, in which the dentary is straight and abruptly decreases posteriorly. The splenial is missing as a consequence of preservation, leaving the Meckelian canal open as widely as that in L. denticulatus. On the ventral side of the subdental shelf, the groove for the dorsal splenodentary articulation indicates that the splenial terminated anteriorly below the sixth anteriormost tooth, leaving a narrow opening for the Meckelian canal facing downwards and medially. The splenial does not cross over the ventral midline, and thus is located totally on the medial side of the jaw.

The lateral surface of the dentary is more convex posteriorly than anteriorly, but is not strongly swollen near the dentary-coronoid articulation. The seven interior alveolar foramina on this specimen represent the total number for this lizard. The first six foramina are small, closely spaced, and located below the first ten teeth; a gap then separates these foramina from the seventh, under the 13th and the 14th teeth. In dorsal view, the lateral surface of the dentary is curved as in L. denticulatus, having the middle part of the jaw slightly concave.



Text-fig. 12. Teiidae, *Leptochamops* sp. (cf. *L. denticulatus*), Oldman Formation, southeastern Alberta; UALVP 29772, nearly complete right denary; (above) lateral view, (below) medial view. Scale = 5 mm.

The tooth row on UALVP 29772 is incomplete, with probably two or three posterior teeth missing. The first two teeth are broken, with only the tooth bases preserved. The next 14 teeth are complete, and are subpleurodont in their mode of attachment. The first seven are conical and their bases are more anteroposteriorly compressed than those that follow. All of the other teeth of this specimen are incipiently tricuspid, having a blunt central main cusp, which is slightly tipped medially, with poorly defined side "cusps" or "side ridges." The posterior teeth are basically cylindrical, but are slightly concave lingually. No replacement pits are evident on this specimen. The basal deposit of cementum is much less heavy than that of Chamops, Socognathus, and the holotype of L. denticulatus. A sulcus dentalis is well-developed along the medial side of the tooth row, and is deeper anteriorly than posteriorly. The tooth row is curved in accordance with the curvature of the dentary.

Another specimen, UALVP 29741, is a tooth-bearing right dentary broken directly behind the 16th tooth position. The splenial on this specimen has its anteriormost part still attached to the dentary, but the posterior part is broken off, as in most fossil teiid specimens. Although the crowns of most of the teeth are partially dissolved, the anterior teeth closely resemble those of UALVP 29772. This character, plus the high-crowned teeth and curvature of the tooth row, indicate that this specimen is also referrable to "Leptochamops sp. (cf. L. denticulatus)."

Discussion: The specimens UALVP 29741 and 29772 represent a Judithian lizard that is closely related to the Lancian L. denticulatus. The curved dentary and tooth row, dorsally concave subdental shelf, and incipiently tricuspid crown pattern all are different from Leptochamops thrinax from the same horizon, but resemble the Lancian L. denticulatus as described by Estes (1964). However, the differences, such as less high-crowned and fewer dentary teeth, much weaker cuspidation, and less heavy basal deposit of cementum on UALVP 29741 and 29772 may indicate separation at a species level. It appears that the two specimens from the Oldman Formation represent a lizard that is more closely related to *L. denticulatus* than to *L. thrinax*, which has broadly tricuspid teeth and a straighter jaw.

Genus Meniscognathus Estes 1964

Type species: Meniscognathus altmani Estes 1964.

Range: Upper Cretaceous, North America.

Disgnosis: As for the type and only known species.

Meniscognathus altmani Estes 1964

Plate 7, Figs. 1-6; Text-fig. 13

Referred specimens: Frenchman Formation, Gryde locality: SMNH P1927.900, P1927.918, P1927.960, P1927.999, P2004.91 (total: 5), incomplete maxillaries; SMNH P1927.887, P1927.895, P1927.903, P1927.915 (total: 4), fragmentary dentaries. Wounded Knee locality: UALVP 29833, fragmentary maxillary.

The following specimens from outside of the study area are also included here, because the BCA specimens document the first occurrence of this lizard in the Hell Creek Formation, and the BTB specimens show significant variation of tooth form that was not clearly known before. Lance Formation, Bushy Tailed Blowout (BTB) locality (UCMP V-5711): UALVP 29832, maxillary; UALVP 29774, 29777, 29834, dentaries. Hell Creek Formation, Bug Creek Anthills (BCA) locality: UALVP 29775, 29779, maxillaries; UALVP 29776, 29831, dentaries.

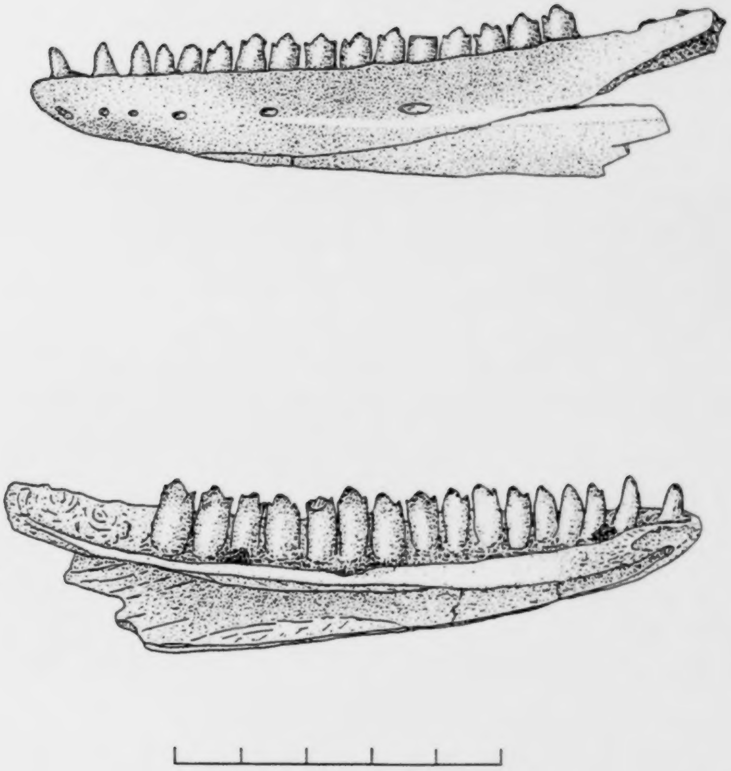
Known distribution: Upper Cretaceous Lance Formation, Wyoming; Hell Creek Formation, Montana; Frenchman Formation, Saskatchewan; all Lancian in age.

Diagnosis (revised from Estes 1983a): Late Cretaceous teiid differing from the closely related Leptochamops denticulatus in having a dentary more slender and more delicately built; dentary teeth short, laterally compressed, and medially concave; tooth crowns broadly bicuspid or weakly tricuspid. Differing from Holocene Kentropyx and related forms in having the marginal teeth low-crowned, less lingually concave, with blunter cusps.

Description: The nine referred specimens from the Frenchman Formation are incomplete maxillaries and dentaries. Most of these specimens are too fragmentary to show details of jaw structure, but preserved teeth show taxonomically significant features on which the referral of these specimens is based.

SMNH P1927.900 is a fragmentary left maxillary from the Gryde locality of the Frenchman Formation. Although incomplete, the specimen has four teeth preserved, and these show diagnostic features of Meniscognathus altmani: marginal teeth low-crowned, medially concave, slightly recurved, and closely spaced. The four teeth are bicuspid and are not strongly compressed labiolingually, as they represent the middle part of a maxillary tooth row (comparable with those on the middle part of the holotype dentary [UCMP 46610, see Estes 1964, fig. 53]). These teeth are pleurodont, with about two-thirds of their height attaching to the lateral parapet of the maxillary.

SMNH P1927.903 consists of a dentary fragment, with four teeth preserved. Differing from the fragmentary maxillary described above, the teeth on this specimen are tricuspid, laterally compressed, and less recurved. These features, in keeping with the slender subdental shelf, indicate that the four teeth are from the posterior part of tooth row. Another dentary fragment (P1927.887), also a posterior part, shows a similar type of tooth form. Six other specimens (SMNH P1927.895, P1927.915, P1927.918, P1927.960, P1927.999, and P2004.91) from the Gryde locality are more fragmentary than the three described above, but are clearly referrable to the same species, on their similar tooth form.



Text-fig. 13. Teiidae, *Meniscognathus altmani*, Lance Formation, eastern Wyoming; UALVP 29774, nearly complete left dentary; (above) lateral view, (below) medial view. Scale = 5 mm.

UALVP 29833 (Plate 7, Fig. 2) is the posterior part of a left maxillary from the Wounded Knee locality of the Frenchman Formation. The maxillary fragment has nine tooth positions, including five teeth and the broken bases of four others. The five teeth are not well-preserved, but still preserve the distinctive features of Meniscognathus, as they are low-crowned, laterally compressed, medially concave, and tricuspid.

In the UALVP collections, four poorly preserved specimens document the first record of Meniscognathus altmani from the Hell Creek Formation, eastern Montana. These specimens are: UALVP 29775, a right maxillary fragment with six well preserved teeth; UALVP 29776, an anterior part of a right dentary with four teeth and bases of six others; UALVP 29779, an incomplete left maxillary with 12 badly worn teeth; and UALVP 29831, an incomplete right dentary having five teeth plus bases and spaces of ten others (a small, newly developed tooth is in the position of replacing the 12th tooth from the front). All of these specimens show a tooth structure comparable to those from the type Lance Formation (see Estes 1964, fig. 53), and are clearly referrable to M. altmani. One of the specimens (UALVP 29779) has heavily worn crowns, but still shows significant features, such as low-crowned, pleurodont, medially concave teeth forming a curved tooth row.

The specimen UALVP 29774 from the BTB locality is an almost complete left dentary, which clearly displays details of the jaw structure and retains the complete tooth count of this lizard (16 complete teeth plus the bases and vacant spaces of five others). The dentary is more delicately built than that of Leptochamops denticulatus. As in the holotype of M. altmani (UCMP 46610), the teeth on this dentary are pleurodont, having about one-third of their height projecting above the lateral parapet. These teeth are low-crowned, closely spaced, and the tooth row is slightly curved in correspondence with the lateral curvature of dentary. In contrast to the holotype, which shows 28 tooth positions, there are a total of 21 in this specimen, including 16 teeth and tooth bases, as well as spaces of five others. The anterior seven teeth (five teeth plus two spaces) are conical, followed by six bicuspid and then eight posterior weakly tricuspid teeth. The bicuspid teeth in the middle part of the tooth row have the crowns bearing a prominent posterior main cusp and a smaller but clearly defined anterior accessory cusp. The posterior teeth are not broadly tricuspid, but have a weak posterior accessary cusp developed, and so that the teeth are only weakly tricuspid. Unlike the corresponding teeth on the holotype, these teeth are straight, not recurved. The short tooth shafts are anteroposteriorly compressed for the anterior conical teeth, but increasingly laterally compressed and lingually concave from the middle bicuspid to the posterior tricuspid teeth. The basal deposit of cementum for the dentary teeth is much less heavy than in Chamops and Leptochamops, as well as other Lancian teiids. A narrow sulcus dentalis is clearly recognizable above the subdental shelf and medial to the tooth row.

Discussion: The teiid Meniscognathus altmani has been previously reported only from the Upper Cretaceous Lance Formation of eastern Wyoming (Estes 1964, 1983a), but not from the Hell Creek Formation of eastern Montana (Estes et al. 1969; Estes & Berberian 1970). The new specimens reported here from the Hell Creek Formation (BCA locality) and the Frenchman Formation (Gryde and Wounded Knee localities) represent the first discoveries of this lizard from Late Cretaceous deposits other than the Lance Formation. These new specimens show that Meniscognathus altmani is a widely distributed Lancian teiid, like Chamops segnis and Leptochamops denticulatus, in the Western Interior of North America.

A problem with the species Meniscognathus altmani as described by Estes (1964) concerns the number of marginal teeth. The species was originally diagnosed as "a teiid lizard with from twenty-one to twenty-eight dentary and about twenty-two (in the only complete specimen) maxillary teeth ...." (Estes 1964: 113). Probably realizing that the tooth count alone is a non-diagnostic for lizard species, Estes (1983a) eliminated the above-cited character from the revised diagnosis, but it remained in the description. The tooth count of this lizard ranges from 21 to 28, unexpectedly wide for a teiid from present understanding of variation in the living species of the group. The normal species range for modern teiids is no more than five tooth positions (Edmund 1969), mostly around three. Perhaps Meniscognathus altmani is exceptional among teiids, with the tooth count varying more than in other species. The nearly complete dentary described above (UALVP 29774) has 21 tooth positions in a full tooth row. Its low number of marginal teeth, in keeping with its straight tooth shaft and more delicately built dentary is suggestive of an alternative interpretation: the subdivision of the "21-phenon" (term "phenon" sensu Mayr & Ashlock 1991) with recurved teeth and the "28-phenon" with straight teeth may indicate that this lizard is sexually dimorphic in terms of tooth count and curvature. But current sample size and poor preservation of most specimens for this taxon do not allow clarification of this alternative interpretation.

Another problem with the species Meniscognathus altmani concerns the morphology of the crowns of the marginal teeth. The species was first diagnosed as having "broadly tricuspid" crowns (Estes 1964), but later revised as having "triconodont or bicuspid crowns" (Estes 1983a). The holotype (UCMP 46610) shows that only the posterior teeth are weakly tricuspid, the middle teeth are bicuspid, while the anterior ones have been broken away. Estes' "broadly tricuspid" characterization was based on a fragmentary maxillary (UCMP 46081) bearing six maxillary teeth (probably posterior teeth). A comparison of the three well-preserved specimens known for this lizard (UCMP 46610, the holotype; UCMP 54266, a nearly complete maxillary; and UALVP 29774, the newly discovered dentary described above) indicates that, in Meniscognathus altmani, the anterior teeth are conical, the middle bicuspid, and the most posterior weakly tricuspid. The diagnosis for this lizard has been revised accordingly.

Among Lancian teiids, Meniscognathus altmani is closely related to Leptochamops denticulatus (Estes 1964, 1983a), and the two together can be placed in the Teiinae (sensu Presch 1983), as evidenced by their resemblances to Kentropyx-Cnemidophorus-Ameiva living group in tooth morphology and jaw structure (Estes 1983a). In regard to jaw shape and tooth form, this group is generally characterised in having a shallow, slender, and elongated dentary in comparison with the closely related Tupinambinae, and generally in having the combination of anterior conical + middle bicuspid + posterior tricuspid teeth, as described here.

Genus Haptosphenus Estes 1964

Type species: Haptosphenus placodon Estes 1964.

Range: Upper Cretaceous, North America.

Diagnosis: As for the type and only known species.

Haptosphenus placodon Estes 1964

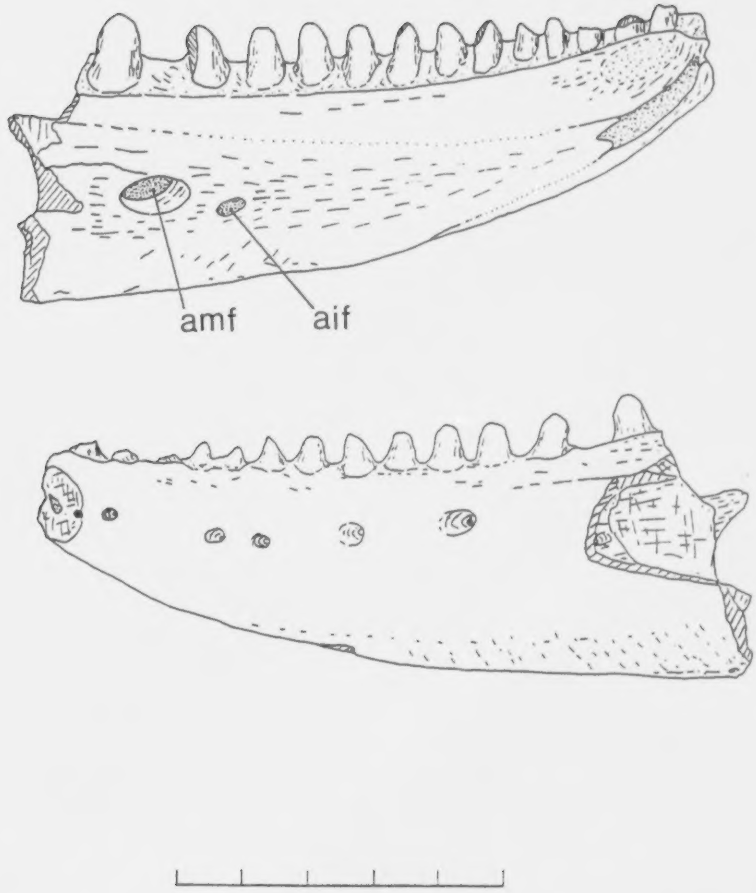
Plate 7, Figs. 7-10; Text-fig. 14

Holotype: UCMP 46035, an almost complete right dentary with 16 tooth positions (the specimen number is misprinted as 46305 in the legend of fig. 54, Estes 1964: 116).

Referred specimens: Frenchman Formation, Gryde locality: SMNH P1920.23, dentary; Wounded Knee locality: UALVP 29771, 29780, dentary fragments. Scollard Formation, KUA-1 locality: UALVP 33921, incomplete dentary.

Known distribution: Upper Cretaceous Lance Formation, Wyoming; Hell Creek Formation, Montana; Frenchman Formation, Saskatchewan; and Scollard Formation, Alberta (all Lancian in age).

Diagnosis (revised from Estes 1964): A Late Cretaceous lizard characterized by the following combination of character states: mandible short and robust, with extensive fusion of splenial, coronoid, dentary and surangular bones; splenial notched anteriorly; dentary teeth short-crowned, laterally compressed, and bluntly tricuspid; sulcus dentalis lost; dentary teeth fused to jaw summit and low lateral parapet, which remains less than one-third of tooth height.



Text-fig. 14. Teiidae, *Haptosphenus placondon*, Frenchman Formation, southwestern Saskatchewan; SMNH P1920.23, left splenodentary; (above) lateral view, (below) medial view. Scale = 5 mm. Abbreviations as in Text-fig. 2.

Description: SMNH P1920.23 from the Gryde locality, Frenchman Formation, consists of an incomplete left mandible (most of the dentary with splenial), which is broken just behind the 13th tooth position. Tapering upward anteriorly, the jaw is short and is closely similar to the holotype (UCMP 46035) in shape.

On its internal side, the dentary bears a weak medial process at its anterior end, forming the main part of the weak mandibular symphysis. The large splenial, covering the extensive internal aspect of the jaw, is fused to the dentary along both the dorsal and ventral splenodentary articulation, but the remnant suture lines are still recognizable. The anterior end of the splenial is notched, and a short anterior opening for the Meckelian canal is developed under the first three dentary teeth. Anteriorly, the ventral splenodentary suture is medial in position, but posterior to the midpoint of the tooth row it is ventral and then laterally located; hence, the posterior half of the ventral suture is not shown in medial view. The splenial has a depression at its central part where two, rather than one (see Estes 1964, fig. 54), Meckelian foramina (anterior inferior alveolar foramen and anterior mylohyoid foramen) open; these are the passageways for Cranial Nerve V_3. The anterior alveolar foramen is smaller and more ventrally located than the anterior mylohyoid foramen (UALVP 33921, a dentary from the Scollard Formation also shows the similar feature).

The external surface of the dentary is slightly convex; it is mostly smooth, but the ventral edge is slightly scarred, reflecting the attachment of hyoid musculature. The six inferior alveolar foramina shown on the specimen are small, rounded, slightly increase in size posteriorly, and are unequally spaced from each other. The last foramen is probably located under the 12th tooth position, where the specimen is broken.

The dentary has 13 partially dissolved teeth preserved; these show no pattern of cusps. The total tooth count for this specimen can be estimated as being no more than 16, as only about four positions can be normally added posterior to the anterior inferior alveolar foramen (see Estes 1964). The tooth row is straight in dorsal view, lacking the curvature seen in

Leptochamops and *Meniscognathus*. A sulcus dentalis is not developed medial to the tooth row, and the remnant lateral parapet is so low (less than one-third of the tooth height) that the term "subpleurodont" is incongruous for this condition; I believe that the term "subacrodont" (sensu Estes 1964) is more appropriate.

Two other referred specimens (UALVP 29771, 29780), both from the Wounded Knee locality of the Frenchman Formation, are dentary fragments bearing badly dissolved teeth. Both of the specimens show splenodentary fusion, with more extensive fusion seen on UALVP 29780, in which the suture is barely recognizable.

Discussion: *Haptosphenus placodon* was originally named and described by Estes (1964) on the basis of several dentary specimens from the Lance Formation, eastern Wyoming. This lizard was later reported from the Hell Creek Formation (Estes et al. 1969; Bryant 1985), eastern Montana, and now from the Frenchman Formation, southwestern Saskatchewan. The newly discovered specimen SMNH P1920.23 resembles the holotype of *H. placodon* (UCMP 46035) in general jaw configuration, in having a subacrodont dentition and splenodentary fusion; therefore, it is clearly referrable to the same species. One difference between the two specimens seems to be that the holotype shows one internal mental foramen for Cranial Nerve V_3, while SMNH P1920.23 has two; however, the holotype is broken at the location of the anterior mylohyoid foramen, and the breakage may have caused the "absence" of this foramen on the specimen. Accordingly, the Frenchman specimen, with two internal Meckelian foramina, represents the natural condition of this lizard.

Estes (1964) referred *Haptosphenus placodon* to the family Teiidae, although he pointed out the two unusual character states of this species: the subacrodont (his "nearly subacrodont") dentition and the fusion of mandibular elements. Initially, he believed that *Haptosphenus* is a tupinambine, stating that "the closest resemblances of *Haptosphenus* seem to be with *Chamops*, differing from the latter both in bone fusion and in having almost acrodont teeth; it may be an aberrant teiid derived from a Chamops-like ancestor" (Estes et al. 1969: 19). But more recently, Estes (1983a) referred Haptosphenus to the Polyglyphanodontinae, an extinct subfamily and commented that "it is possible that when skull material is known that it will prove referable to an extinct family; on the basis of general proportions of the teeth and jaw, however, it possible that it is a member of the Polyglyphanodontinae. As it retains the presumably primitive triconodont [tricuspid] tooth type it would be the most primitive of the group if properly referred" (Estes 1983a: 83). It is difficult to clarify further the intra- and supra-generic relationships of this lizard until more complete materials are found.

The Lancian Haptosphenus is indeed highly specialized, with both fusion of the mandibular elements and a subacrodont dentition (Estes 1964, 1983a; Estes et al. 1969), and its relationship with modern teiids is much less clear than that of other teiids from the same horizon (Estes & Baez 1985). The fusion of some mandibular elements occurs independently in several modern lizard families (Xantusiidae, Iguanidae, Gekkonidae) that are obviously remote from Haptosphenus. This feature has not been reported from any modern teiids (see later discussion) to which Haptosphenus is possibly related; however, some Cretaceous teiids show the potiential development of this feature: in Sphenosiagon, the large splenial is firmly articulated with the dentary, although the mandible is lightly built; and in Gerontoseps, the splenial is partially fused to the dentary along the dorsal splenodentary suture (see Gao & Fox 1991 and relevant discussion in this paper). In spite of these similarities, the relationships of Haptosphenus with the above-mentioned two teiids are still obscure: several conspicuous differences, such as the form and mode of attachment of the marginal teeth (Sphenosiagon: slender jaw, unicuspid and high crowned teeth; Gerontoseps: deep sulcus dentalis and subpleurodont teeth) make a close relationship unlikely.

Another unusual character of this lizard, the subacrodont dentition, is associated with the loss of the sulcus dentalis and lateral parapet of the dentary, and is commonly understood as a more primitive condition than the true acrodont condition (also see Gauthier et al. 1988 for a different interpretation of the acrodont condition). Among lizards (including amphisbaenians), the true acrodont condition is independently developed in iguanians, and trogonophid and oligodontosaurid amphisbaenians (Zangerl 1944; Gans 1958, 1978; Estes 1975).

It is clear that acrodonty in the highly specialized Acrodonta Cope 1864 (= Chamaeleonoidea Moody 1980, see Estes et al. 1988) is unlikely to be associated with the subacrodonty of certain teiids, such as Haptosphenus, as the relationships of the two groups are remote, as reflected in their classification in two different infraorders.

Comparing the subacrodonty of Haptosphenus with the acrodonty of amphisbaenians raises another problem. A sister group relationship of amphisbaenians with Teiidae (sensu lato, = Teiioidea Estes et al. 1988) has been suggested by Boulenger (1884), Bogert (1964), and Bohme (1981), and supported by several other authors (Saint Girons 1968; Lecuru 1969; Presch 1975; Schwenk 1988). However, the subacrodont condition in Haptosphenus is evidently nonhomologous to acrodonty in those oligodontosaurid and trongonophid amphisbaenians, because the more primitive pleurodont condition occurs in both Teiidae (sensu lato) and Amphisbaenia (see Estes 1983a), and the two groups are currently understood as separate monophyletic taxa (Estes et al. 1988).

Based on the available evidence from jaw shape and tooth form, it seems more reasonable to accept Estes' (1964, 1983a, 1985) assignment of Haptosphenus as a member of Teiidae than of any other lizard family. From proportions of the teeth and jaws, Estes (1983a, 1985) also suggested a possible relationship of this lizard to the subfamily Polyglyphanodontinae (sensu Estes 1983a), which includes two genera (Polyglyphanodon and Adamisaurus) also having a subacrodont dentition. Polyglyphanodon is known from the Lancian North Horn Formation, Utah (Gilmore 1940, 1942b, 1943b), and Adamisaurus is from the Campanian Djadochta Formation of the Gobi Desert (Sulimski 1972, 1978). The latter two lizards show a more close resemblance to each other in terms of crown pattern than either does to Haptosphenus. At least, the tooth crowns of the former two genera are more or less transversely expanded, while those in Haptosphenus are tricuspid. In addition, Adamisaurus clearly shows well-developed resorption pits, while the subacrodont teeth of Haptosphenus are apparently not replaced. These differences certainly throw doubt on the inclusion of Haptosphenus in the Polyglyphanodontinae. Here, I draw attention to the close resemblance of this lizard to the living form Draceana, as these two lizards show the following similarities: 1) dentary short, robust, and strongly tapering upward anteriorly; 2) splenial large, posteriorly extending to lateral surface of the jaw; 3) location and number of internal mandibular foramina comparable; 4) mandibular elements fused or tending to be fused; 5) subacrodont tooth attachment. If these similarities are phylogenetically significant, Haptosphenus may be a member of the Teiinae (sensu Estes 1983a).

Genus Stypodontosaurus n. gen.

Type species: Stypodontosaurus melletes n. sp..

Range: Upper Cretaceous, North America.

Diagnosis: As for the type and only known species.

Etymology: stypos + odontos + sauros (Gr., m.), meaning stumpy-toothed lizard, in reference to the short and stout teeth of this lizard.

Stypodontosaurus melletes n. sp.

Plate 8, Figs. 1-2; Text-fig. 15

Holotype: UALVP 29844, a nearly complete right dentary having 16 teeth and the base of another.

Type locality and horizon: KU-A1 locality (Lillegraven 1969), Red Deer River Valley near the village of Scollard, central Alberta; Upper Cretaceous Scollard Formation (Lancian in age).

Known distribution: Type locality only.

Diagnosis: A Late Cretaceous teiid differing from other fossil and Recent teiids in having the following combination of character states: dentary greatly elongated and robust; subdental shelf deep and strong, maximum depth about equal to tooth height; sulcus dentalis narrow and deep; dentary teeth short, stumpy, and widely spaced from each other; tooth crowns unicuspid, but having a well-defined crest enclosing a horseshoe-shaped medial surface; tooth attachment subpleurodont, with over half of tooth height projecting above lateral parapet.

Etymology: melletes (Gr., m.), meaning "delayer", in reference to its late geologic occurrence in the Late Cretaceous, and its delayed recovery in 1991 from the screen-washed concentrate collected in 1960s.

Description: The holotype and only known specimen is a well-preserved right dentary, lacking only its posteroventral part. The dentary is basically straight, but is curved anteriorly at the mandibular symphysis. The shape of the dentary indicates that the mandible of this lizard is shallow, elongated, but robustly built.

Medially, the dentary bears a sturdy subdental shelf, which is greatly deepened over the anterior two thirds of the length of the specimen, but abruptly reduced over the posterior one third. The maximum depth of the shelf is about the same as the tooth height. The anterior end of the shelf bears a robust medial process, which forms the main part of the strong mandibular symphysis, although the anterior tip of the jaw is very shallow. The ventral surface of the shelf bears a well-developed groove for the splenodentary articulation. The groove shows that the splenial (missing on the specimen) extended well anteriorly, to beneath the sixth tooth position. The dorsal edge of the subdental shelf, which is straight in medial view, is developed as a sharp and strong ridge along the medial border of the narrow, deep sulcus dentalis. The Meckelian canal is strongly restricted under the first five tooth positions, where the fissure-like anterior opening of the canal is located, but abruptly increases in depth and width posteriorly from the sixth tooth.

The dentary teeth are short, stout, pillar-like, and widely spaced from each other. With a faint central cusp that is slightly turned medially, the tooth crowns can be technically termed unicuspid, but characteristically have well-defined side ridges (crests) running laterally from the cusp, then down and medially, encircling a more or less horseshoe-shaped area on the medial side of the crown. The tooth attachment is subpleurodont, with the tooth bases attached to the low lateral parapet, which is less than half of the tooth height. At the tooth bases, the basal deposit of cementum is extensive as in most Cretaceous and Recent teiids. The size of the dentary and the absence of replacement pits indicate that the holotype and only known specimen represents a mature individual, in which tooth replacement has been suppressed. A dorsal view of the specimen shows that the dentary tooth row is straight for the posterior 12 teeth, but slightly curved towards the symphysis for the first five anterior teeth. The dentary has 17 tooth positions (16 complete teeth and the tooth base of another), the complete tooth row of the holotype.

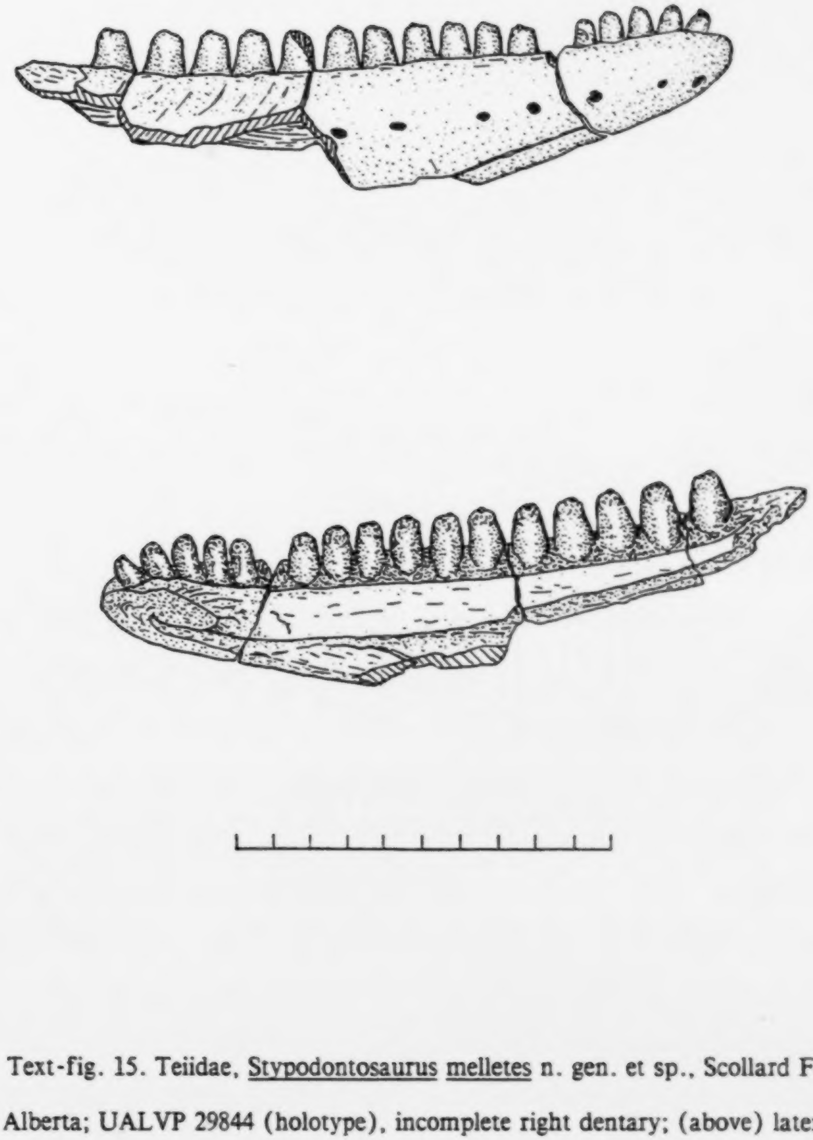
The lateral surface of the dentary is slightly convex for the anterior two-thirds of the bone, but the posterolateral part bulges strongly, a result of the posterior width of the Meckelian canal. The posteroventral part of the dentary is missing, but the remainder shows that the ventral border turns strongly towards the medial side of the jaw; accordingly, the ventral splenodentary suture faces ventromedially. The lateral surface shows seven inferior alveolar foramina, which are small, rounded, and more or less evenly spaced in a horizontal row.

Discussion: UALVP 29844 is the holotype and the only known specimen of this new teiid from the Scollard Formation. The specimen shows several teiid synapomorphies, including hypertrophy of the splenial (indicated by the widely open Meckelian canal) and the conspicuous deposit of cementum around the tooth bases (see Estes et al. 1988 for citations). Other character states, such as a well-developed sulcus dentalis and subdental shelf, and the subpleurodont tooth attachment, are also highly indicative of affinity with the family Teiidae. The crowns of the dentary teeth are in some degree similar to that of the African cordylid Cordylurus, but differences of the two genera in geographical distribution and morphological characters mentioned above indicate that this similarity is probably convergent.

Compared with other fossil and Recent teiids, the most conspicuous features of this new lizard are the extremely deep subdental shelf, and the short, stout teeth with unique crown pattern described above. A deep subdental shelf is usually seen in lizards that have short and deep jaws (e.g., Glyptogenys, see above), but is uncommon in those lizards having shallow and elongated jaws. A strong subdental shelf certainly will make the jaw more solidly built, and hence strengthen the biting mechanism. This type of crushing jaw mechanism is commonly associated with short-crowned, stout teeth in other teiids, such as Chamops, Tupinambis, and Dracaena.

The tooth crowns of this lizard are laterally compressed, having a tiny central cusp that turns medially and lateral ridges that curve down and medially. This pattern is different from those of Judithian teiids, such as Gerontoseps, in which a narrow crown bears a rounded cusp with weakly developed lateral ridges. It is difficult, at this stage, to determine whether this crown pattern is derived from a tricuspid condition in which ridges linked the side cusps with the main cusp, or is a more primitive condition in which there were no side cusps originally. The dentary teeth show no replacement pits at the tooth bases, perhaps as a consequence of age, in which tooth replacement was suppressed.

The jaw configuration and the tooth form of this new lizard are so different compared to other known teiids that I find no evidence on which to make a reasonable interpretation about relationships below the familial level. However, it may be possible to include this form with the problematic subfamily Polyglyphanodontinae, which includes several Late Cretaceous teiids having aberrant tooth forms.



Text-fig. 15. Teiidae, Stypodontosaurus melletes n. gen. et sp., Scollard Formation, central Alberta; UALVP 29844 (holotype), incomplete right dentary; (above) lateral view, (below) medial view. Scale = 10 mm.

Genus Alocosaurus n. gen.

Type and only known species: Alocosaurus johnstoni n. sp..

Range: Upper Cretaceous, North America.

Diagnosis: As for the type and only known species.

Etymology: alox + sauros (Gr. m.), meaning furrow lizard; in reference to the furrow-like grooves in the upper and lower jaws of this lizard.

Alocosaurus johnstoni n. sp.

Plate 8, Figs. 3-4; Text-fig. 16

Holotype: UALVP 29791, incomplete right dentary having three complete, two broken teeth, and the spaces for three others.

Type locality and horizon: Outcrop of the Upper Cretaceous Oldman Formation near Irvine, about 40 km east of Medicine Hat, southeastern Alberta, Canada.

Referred specimens: UALVP 29793-29795, 29800, 29808-29809 (total: 6); topotypic tooth-bearing maxillaries and dentaries from the Irvine locality.

Known distribution: Upper Cretaceous Oldman Formation (Judithian), southeastern Alberta, Canada.

Etymology: The species name is to Dr. P. A. Johnston, who was the first to recognize the lizard as a new species (Johnston 1977).

Diagnosis: A Judithian species differing from other teiids in having the following combination of character states: dentary greatly elongated, having numerous external foramina often extending posteriorly as furrow-like grooves; anterior half of Meckelian canal widely open; marginal teeth short-crowned, conical, approaching subacrodont condition, and with large replacement pits.

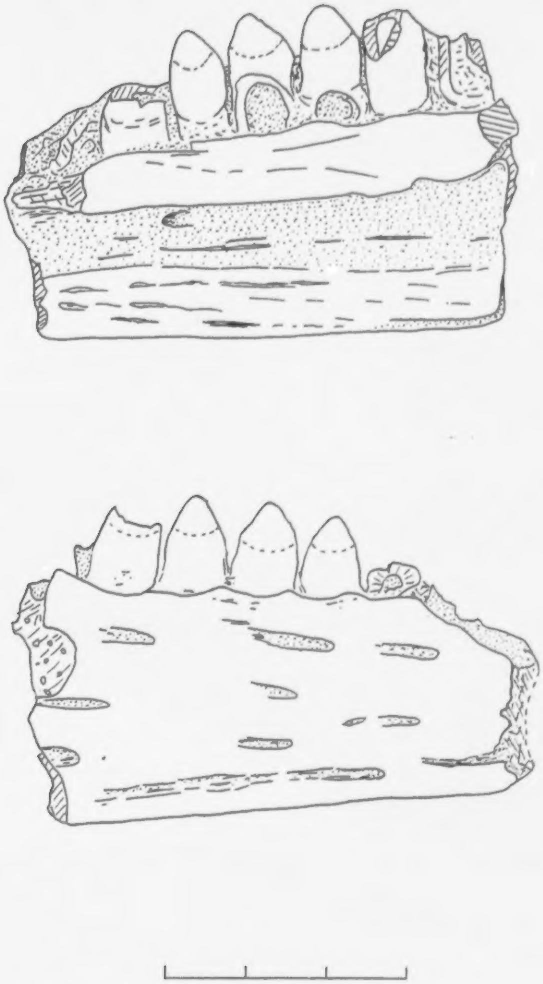
Description: The dentary of this lizard is shallow, greatly elongated, and rather massively built, especially in the anterior half where the Meckelian canal is greatly narrowed and the thickness of the bone is increased. Although robust, the dentary is well vascularized, with numerous tiny canals penetrating the bone anteroposteriorly and opening at the external surface of the dentary through tiny foramina with furrow-like grooves that extend posteriorly.

The medial side of the dentary bears a strong subdental shelf, which has a prominent dorsal ridge bordering the well defined sulcus dentalis. The shelf runs horizontally, in contrast to the curved shelf in Leptochamops and its related genera. With the splenial being unpreserved, the Meckelian canal is widely open, clearly showing its internal structure: the inferior alveolar canal is developed in the anterior half of the dentary, and the posterior inferior alveolar foramen opens close to the midpoint of the tooth row. Unlike other fossil and Recent teiids, Alocosaurus lacks a groove on the ventral side of the subdental shelf for the dorsal splenodentary articulation. Instead, a shallow depression at the anterior end of the dentary seems to indicate that the splenial was loosely attached to the dentary and terminated anteriorly below the fifth tooth position. The posterior half of the Meckelian canal is greatly enlarged, having an arched roof and a sharp ventral edge of the subdental shelf.

The dentary teeth on most specimens are poorly preserved, having partially dessolved crowns. However, UALVP 29800 (a dentary fragment with two nicely preserved teeth and broken bases of four others) clearly shows that the marginal teeth of Alocosaurus are short-crowned, conical, lack accessary cusps or side ridges, and are closely spaced from one another. The tooth attachment approaches a subacrodont condition, as the labial parapet of dentary is reduced to equal the height of the lingual side. However, this condition is different from that in Haptosphenus and Sphenosiagon, since a sulcus dentalis is well developed and the teeth seem to be set in an extremely shallow dental groove. The tooth count for the complete dentary tooth row is uncertain, but can be estimated as about 25 or more by comparing UALVP 29794 with UALVP 29795, which separately show the tooth positions in front of and behind the posterior interior alveolar foramen in the Meckelian canal.

Large replacement pits are frequently developed lingually at the tooth bases, indicating an "intermediate type" of replacement pattern (Edmund 1969). Vacant tooth positions are often shown in probably old individuals, as, for example, on specimens UALVP 29793, 29795-29796.

UALVP 29808-29809 are the only two maxillaries known for Alocosaurus and are more poorly preserved than the dentary specimens at hand. The first specimen (UALVP 29808) is the anterior part of a left maxillary, bearing a high nasal process. The lateral surface of the nasal process is pitted with numerous, scattered, ethmoidal foramina, although those close to the ventral border forming a row of superior alveolar foramina. The dorsal edge of the maxillary is lower posteriorly, form a gentle slope in lateral view. Internally, the maxillary bears a slender supradental shelf, which has a ventral ridge that borders the dental gutter medially. The internal surface of the maxillary bears fossae for the naris, and for the articulation with palatal bones. UALVP 29808 shows the first five tooth positions, including two complete teeth and the bases of three others. The first tooth is complete, short and conical as seen in the dentaries. The third tooth is malformed, with the tooth crown bent medially at an angle of about 90 degrees. A similar condition is also seen in a dentary specimen (UALVP 29794). The mode of attachment of the maxillary teeth is the same as the dentary teeth, subpleurodont approaching a subacrodont condition. Large replacement pits are also developed at the medial side of the tooth bases, and the bases are heavily cemented as in other teiids.



Text-fig. 16. Teiidae, *Alocosaurus johnstoni* n. gen. et sp., Oldman Formation, southeastern Alberta; UALVP 29791 (holotype), incomplete right dentary; (above) lateral view, (below) medial view. Scale = 5 mm.

The second specimen, UALVP 29809, also a left maxillary fragment, is obviously from an individual that is older than UALVP 29808, judging from its size and robustness. The lateral surface of this maxillary also shows mental foramina having long grooves that extend posteriorly, as seen on the dentaries.

Discussion: Alocosaurus is an aberrant lizard, which displays certain features notably different from those of other known scincomorphans. These features include: short-crowned, bluntly conical teeth set in a extremely shallow dental groove, although approaching a subacrodont condition; a highly-vascularized dentary having numerous external foramina extending posteriorly as furrow-like grooves on the external surface; and no tongue-groove interlocking for the splenodentary articulation. These character states are so different from those of other teiids as to make its familial assignment uncertain; however, the wide Meckelian canal, large replacement pits, and strong subdental shelf suggest a teiid relationship. The large replacement pits resemble those of teiinine lizards that Estes (1983a, fig. 23) figured. Therefore, Alocosaurus is tentatively referred to the family Teiidae. It is only known from very fragmentary jaw materials, and further study on better preserved specimens in the future would be beneficial to understand this taxon.

As mentioned above, one of the distinctive characters of Alocosaurus is the vascularization of the maxillary and dentary. The numerous elongate foramina on the lateral surface of the jaws may indicate many nerve endings and blood vessels, and hence, may well indicate a burrowing life style with sensitive nerve endings on the jaws. However, this interpretation currently lacks support from evidence other than jaw structures.

Although the teeth in most specimens of Alocosaurus are partially dissolved, one specimen (UALVP 29800) with two nicely preserved teeth clearly shows them to be short-crowned, conical, and closely spaced. The two malformed teeth on UALVP 29808 and 29794 are new and obviously from two relatively younger individuals. The lopsided development of the two teeth is apparently the result of mechanical damage, as one tooth still shows a crack on the base.

All the specimens currently known for Alocosaurus are fragmentary dentaries and maxillaries. The poor preservation of these specimens may result from both mechanical and chemical erosion in relatively long distance transportation, as indicated by partially dissolved teeth and rounded edges of the bones (rather than fresh breakage from screen washing in collecting).

Family Scincidae Gray 1825

Genus Penemabuya n. gen.

Type species: Penemabuya antecessa n. sp.

Range: Upper Cretaceous, North America.

Diagnosis: As for the type and only known species.

Etymology: pene (L.), near, almost; mabuya (L.), a kind of skink lizard.

Penemabuya antecessa n. sp.

Plate 9, Figs. 1-3; Text-fig. 17

Holotype: UALVP 29789, incomplete right dentary having six teeth and the broken bases as well as vacant spaces of 16 others.

Type locality and horizon: MR-6 locality, Verdigris Coulee, approximately 30 km east of the village of Milk River, southern Alberta; upper member of the Milk River Formation (Aquilan in age), Upper Cretaceous.

Referred specimens: UALVP 29788, 29827-29828, and several unnumbered jaw fragments.

Known distribution: Upper Cretaceous Milk River Formation, southern Alberta, Canada.

Diagnosis: A Late Cretaceous skink closely resembling the Recent Mabuya, but differing from the latter by the following combination of character states: dentary less elongated, with fewer, and sharply pointed teeth; anterior one-third of Meckelian canal open, posterior two-thirds covered by splenial; subdental shelf more prominent.

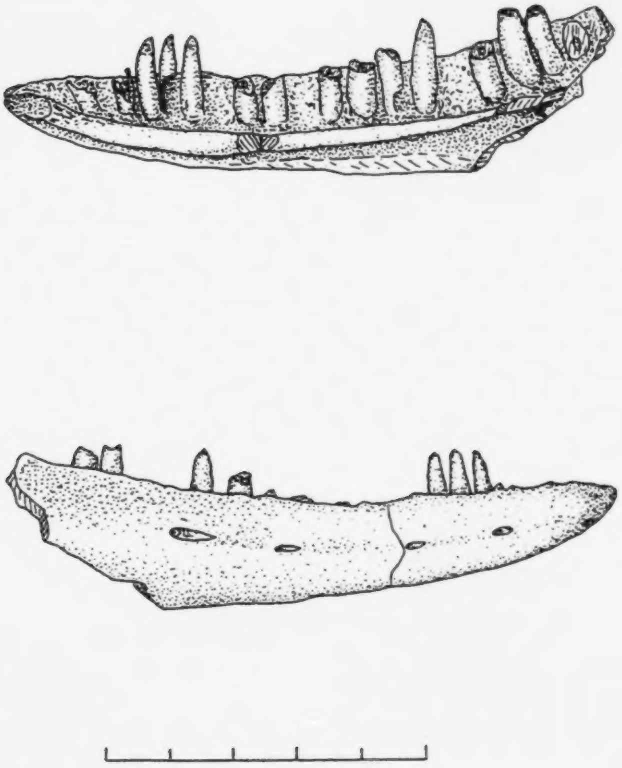
Etymology: antecessor (L.), meaning forerunner, in reference to the pre-*Mabuya* dentary morphology of this lizard.

Description: Two specimens of this lizard, the holotype, UALVP 29789, and UALVP 29788, are especially well preserved. The holotype is an almost complete right dentary, with only the very posterior end of the bone missing. It is shallow, slender, and greatly elongated. Medially, the specimen bears a slender but prominent subdental shelf, which gently curves upward and is diminished posteriorly. The anterior tip of the shelf turns mediodorsally, forming most of the delicate mandibular symphysis. Below the subdental shelf, the Meckelian canal is extremely narrow along its anterior half but slightly increases in its depth posteriorly, beneath the upward curving subdental shelf. Judging from the articulation surface, the missing splenial seems to have been a shallow and slender bone that medioventrally covered the posterior two-thirds of the Meckelian canal, leaving the anterior third open ventrally. Posteriorly within the Meckelian canal, the posterior interior alveolar foramen opens below the 20th tooth position, and no intramandibular septum is developed in the canal.

The dentary teeth of this skink are pleurodont, with about two-thirds of the tooth height attached to the well-developed lateral parapet of the jaw. There are 22 tooth positions on the preserved part of the dentary; possibly only the two most posterior teeth are missing (judging from the posterior extremity of subdental shelf that corresponds to the termination of tooth row). On the holotype, four teeth are completely preserved (seventh through the ninth, and the 17th from the front), and two are nearly complete with just the tips broken. The tooth shafts are slender and the crowns are unicusped and pointed, with weak medial striations. There is no notable change of tooth structure from anterior to posterior along the tooth row, except that the anterior teeth have slightly recurved crowns. The basal part of the eighth tooth has been largely resorbed, but its upper half is still functional and weakly attached to the parapet at its base. The 20th and the 21st tooth positions have only the top part of the teeth broken, while the rest of the tooth row consists of either tooth bases or teeth that are entirely missing.

The lateral surface of the dentary is smooth, showing no sculpture. A row of unequally spaced inferior alveolar foramina (five on the holotype) opens laterally, and each foramen shows a certain degree of anterior elongation. Below the foramina, the edge of the dentary turns sharply medially, tending to enclose the Meckelian canal, and forming a more or less flat surface for the anterior two-thirds of the dentary ventral border.

Another well-preserved specimen, UALVP 29788, consists of a nearly complete right dentary showing all of the positions in the tooth row. On this specimen, seven teeth are complete, and another 17 are tooth spaces or broken bases, making the full tooth count of this specimen 24. The specimen is referrable to Penemabuya antecessa on its close resemblances to the holotype (UALVP 29789) in shape and structure of dentary, and in tooth morphology. However, UALVP 29788 has heavy deposits of cementum at the tooth bases, and shows an unusual pattern of tooth replacement (Plate 9, Fig. 3) that is different from that in the holotype. The heavy basal deposits of cementum is probably an age character, and the tooth replacement in this specimen may represent an abnormal condition. In this specimen, the sixth and the seventh teeth from the back are new replacement teeth that have developed posteromedially to the replaced teeth and have already reached the functional height of the tooth row, but one old tooth shows no sign of being resorbed and is functional together with the new tooth. This type of tooth replacement was not recorded in Edmund (1969), and apparently represents an abnormal condition.



Text-fig. 17. Scincidae, Penemabuya antecessa n. gen. et sp., upper member of Milk River Formation, southern Alberta; UALVP 29789 (holotype), incomplete right dentary; (above) lateral view, (below) medial view. Scale = 5 mm.

Discussion: Osteologically, the family Scincidae is characterized by several synapomorphies, including a jugal-squamosal contact, a closure of the supratemporal fenestra, and a medial extension of the palatines to form a bony secondary palate (see Estes et al. 1988). Although these characters are unavailable for the screen-washed materials in this study, a combination of the following character states on the jaws of this lizard is strongly indicative of its affiliation with the Scincidae: an elongated dentary, narrow Meckelian canal, which tends towards complete closure; a well-defined subdental shelf; and a pleurodont, Mabuya-like tooth form.

Among modern scincid lizards, Eumeces Wiegmann 1834 (Scincinae) and Mabuya Fitzinger 1826 (Lygosominae) are the two most widely distributed genera (Mattison 1989). Besides the character states discussed by Greer (1970), I here draw attention to differences between the two genera in jaw structure and tooth form. These differences are: 1) the dentary of Mabuya is generally much more slender and elongated than that of Eumeces; 2) the spenial is much more reduced in the former, and does not extend anteriorly beyond the midpoint of the tooth row; 3) the Meckelian canal of Mabuya is often closed anteriorly by fusion of the dentary, but is commonly open in Eumeces; 4) the marginal teeth of Mabuya are cylindrical and pointed, while in Eumeces, the tooth shafts are more or less compressed anteroposteriorly, and the crowns are wider and have lateral crests, with strong medial striations; 5) tooth replacement is more frequent in Mabuya than in Eumeces, correspondently, the former has a basal foramen at each tooth base, while the latter does not.

A comparison of the new skink from the Milk River Formation with Recent Eumeces and Mabuya suggests that the new lizard is probably more closely related to the Lygosominae than to the Scincinae as indicated by its close resemblance to Mabuya in configuration of dentary and crown pattern of teeth. As mentioned above, the anterior half of the Meckelian canal in modern Mabuya is closed by fusion of the dentary, while the splenial is greatly reduced, covering the posterior half or less of the canal. In the new skink Penemabuya, the

Meckelian canal remains open, but clearly shows a tendency to be closed by medial extension of the ventrolateral edge of the dentary. The splenial, although narrow and small, covers the posterior two-thirds of the Meckelian canal, leaving the anterior one-third open ventrally. According to Greer (1970), having a larger splenial and an open Meckelian canal are more primitive conditions within the Lygosominae, and hence, the new lizard may represent a pre-Mabuya Cretaceous form of the group. Most Recent Australian lygosomine skinks also have closed the Meckelian canal by fusion of the dentary, supporting the above interpretation.

Mabuya is an important genus of skinks, having a great number of species and almost a cosmopolitan distribution. There are about 85 species that have been recognized for this genus, 20 of them in southern Asia, nine species in Central and South America, including the West Indies, and the rest in Africa, Madagascar, and several islands in the Indian Ocean (data from Greer 1970; Peters et al. 1986; Mattison 1989). The geographical origin of Mabuya is an open question, although Dunn (1936) noted the close relationship of the New World species with the African species of the genus; Darlington (1957: 194) believed that the New World Mabuya "may have come from Africa on drift;" and Greer (1970: 180) noted the difficulty of determining "whether the group arrived from Asia via the Bering Land Bridge or from Africa by over-water rafting," but favored the latter possibility. Greer (1970: 180) also stated that "the lack of diversity of the New World species may indicate that the group has not been in the New World very long." Certainly, an equally strong argument could be made that the great diversity of the group in Africa may indicate a more successful radiation, which is likely an event that happened more recently and in a place other than its place of origin. To look for its place of origin, more weight might be put on where the group retains more primitive characters than where it has a greater diversity of species, since the evolutionary rate of the group may well have increased greatly in a newly adapted environment (Matthew 1915).

The newly recovered Mabuya-like skink from the Upper Cretaceous Milk River Formation at least indicates that the Scincidae have been on the North American Continent since early Campanian time (some 83 Myr ago), and may count in support of a possible northern continental origin for the group. Nonetheless, the nearly worldwide distribution of the Scincidae hints at a Cretaceous radiation, and possibly a long evolutionary history before that; this interpretation is now well corroborated with the new discovery of primitive _Mabuya_-like skink from the Upper Cretaceous Milk River Formation.

Genus Orthrioscincus n. gen.

Type species: Orthrioscincus mixtus n. sp..

Range: Upper Cretaceous, North America.

Diagnosis: As for the type and only known species.

Etymology: orthrios + skinkos (Gr. m.), meaning early skink.

Orthrioscincus mixtus n. sp.

Plate 9, Figs. 4-6; Text-fig. 18

Holotype: UALVP 29747, incomplete left dentary having seven teeth and tooth bases as well as spaces for ten others.

Type locality and horizon: Outcrop of the Oldman Formation near Irvine, in S 31, Tp. 11, R 2, W 4, about 40 km east of Medicine Hat, southeastern Alberta; Upper Cretaceous Oldman Formation (Judithian in age).

Referred specimen: UALVP 29904, a nearly complete right dentary bearing 19 tooth positions.

Known distribution: Upper Cretaceous Oldman Formation, southeastern Alberta, Canada.

Diagnosis: A Late Cretaceous scincoid lizard having dentary structures broadly resembling those of the Recent Eumeces group, but with tooth morphology more similar to the cordylid gerrhosaur group. Differing from other scincoids of the same age as follows: subdental shelf slender, sulcus dentalis poorly defined, dentary teeth bicuspid. Differing from

Gerrhosaurus Wiegmann 1828 in having anterior cusp less clearly separated from the posterior main cusp, and main cusp not recurved.

Etymology: mixtus (L.), referring to the combination of Eumeces-like characters of the dentary and Gerrhosaurus-like teeth of this lizard.

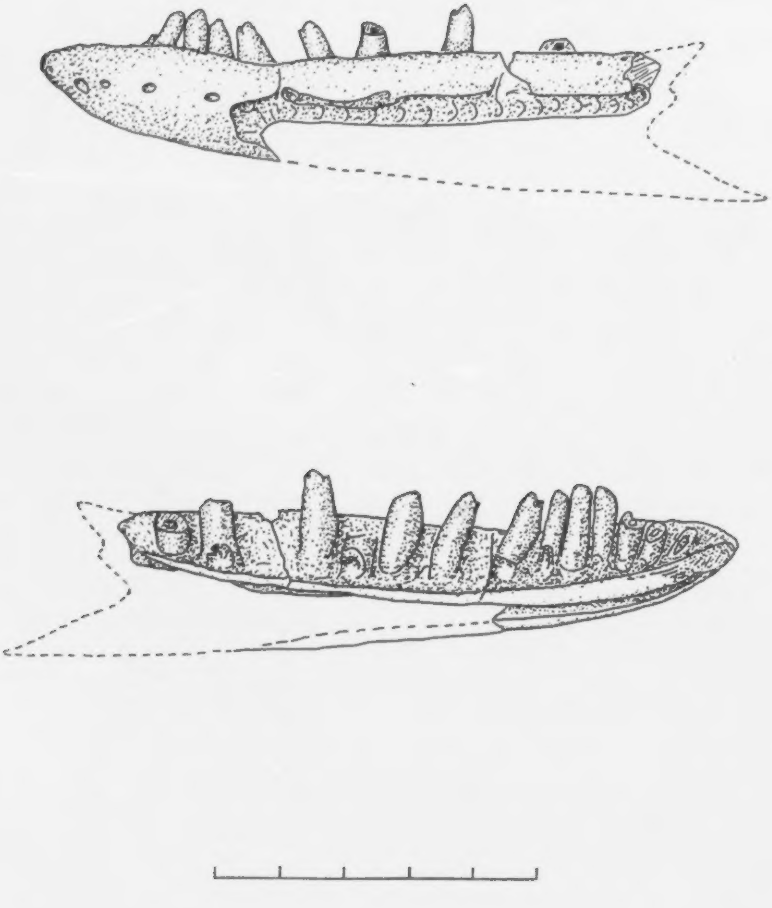
Description: The holotype (UALVP 29747) is a tooth-bearing left dentary, which has only the posteroventral part missing. The specimen is designated as the holotype because it clearly shows the tooth form of this new lizard, while the referred specimen UALVP 29904, a right dentary, has less well-preserved teeth but nearly shows the complete configuration of the dentary.

The dentary is shallow, straight, elongated, and lightly built, as in most Recent scincoids. On its medial side, the dentary bears a slender subdental shelf, the maximum depth of which is much less than one-third of the tooth height, and the shelf strongly curves dorsally at its anterior end. These proportions closely resemble those of the Recent scincid Eumeces in comparable parts. Above the subdental shelf and medial to the tooth row is a weakly developed sulcus dentalis, which forms a shallow trough. Below the shelf, the Meckelian canal posteriorly has a maximum depth about equal to the tooth height, but the canal becomes increasingly narrow and faces ventromedially towards the anterior end of the jaw. The posterior interior alveolar foramen opens into the Meckelian canal under the 14th tooth position (between the 13th and the 14th on the holotype).

Both UALVP 29747 and 29904 document the complete dentary tooth row; the two specimens together indicate that the dentary tooth count of this lizard is variable, ranging at least between 17 (on the holotype) and 19 (on UALVP 29904). The tooth form is clearly shown on the holotype, while the crowns of the UALVP 29904 are partially dissolved, showing no detail about the cusp pattern. The dentary teeth are pleurodont, with about one-third of the tooth height projecting above the lateral parapet of dentary. The broken tooth shafts show that the anterior and the middle teeth are slightly compressed anteroposteriorly, but the posterior ones (the last four or five) are cylindrical. In general, the teeth are close to one another along the tooth row, but the spacing is variable as the result of tooth replacement. The first five or six teeth are slightly procumbent, are conical, and are slightly shorter than those mid-way along the tooth row. The posterior teeth are slightly stronger than the middle teeth. The crowns of the middle and posterior teeth are bicuspid, having a small, pointed, low anterior cusp, and a high and blunt posterior main cusp, which is weakly striated on its medial surface. This particular cusp pattern resembles that of some Recent scincoids, such as Gerrhosaurus (Cordylidae).

Both the holotype and UALVP 29904 show that several teeth have developed an excavation posteromedially at the tooth bases. This indicates an intermediate replacement pattern (Edmund 1969), which differs from the "iguanid pattern" in having the replacement tooth developed posteromedial to (rather than directly within) the old teeth, and from the "varanid pattern" in having a resorption cavity, although this is shallow. On the holotype, the ninth tooth is obviously loosely attached to the dentary, with the tooth base being slightly off the main line of the tooth row. Behind this tooth is a large space for the tenth tooth, which has already fallen from the tooth row. This abnormal condition of the ninth dentary tooth is possibly the result of mechanical damage, because this tooth is large enough to have been fully functional, but would have been attached to the lateral parapet in the normal condition.

The lateral surface of the dentary is incomplete on the holotype, but was apparently smoothly convex like that in UALVP 29904. Five small inferior alveolar foramina are present, and are unevenly spaced along a horizontal row. The last foramen is located lateral to the 13th tooth position, close to the posterior interior alveolar foramen within the Meckelian canal.



Text-fig. 18. Scincidae, Orthrioscincus mixtus n. gen. et sp., Oldman Formation, southeastern Alberta; UALVP 29747 (holotype), incomplete left denary; (above) lateral view, (below) medial view. Scale = 5 mm.

UALVP 29904 is a nearly complete right dentary from the type locality. This specimen resembles the holotype in general morphology, but all the teeth (19 in total) have the crowns partially dissolved. On the basis of its similar dentary configuration, this specimen is referrable to the same species as the holotype; however, the poorly preserved tooth crowns make this referral somewhat uncertain. Perhaps later discovery of better preserved specimens will verify its taxonomic position.

Discussion: The new lizard Orthrioscincus from the Oldman Formation shows a combination of a Eumeces-like dentary configuration with a Gerrhosaurus-like tooth form. This mosaic of characters provides sufficient evidence for placing it in the Scincoidea. Referral at a familial level is somewhat uncertain, however, since the two families within the Scincoidea (Scincidae and Cordylidae) are primarily distinguished from each other by skull and external structures (see Estes et al. 1988) that are not preserved in the Oldman specimens. However, this lizard could be referred to the Scincidae on biogeographic evidence and the Eumeces-like shape of its dentary, with its tooth form convergent on that of Gerrhosaurus.

Recent gerrhosaurine lizards are widely distributed in Africa, but are unknown from other places of the world. The limited, Miocene, fossil record of this group is also African (see Estes 1983a). Discovery in the Oldman Formation of Orthrioscincus with its Gerrhosaurus-like dentition reveals the following possibilities:

1) Ancestral gerrhosaurines once had a much wider geographical distribution than they have today. Orthrioscincus may represent one of the primitive member of the group that occupied similar ecological niches in North America as does Gerrhosaurus in Africa today. Indeed, with reference to tooth form only, I would place Orthrioscincus in the gerrhosaur group (Cordylidae) rather than Scincidae. However, the jaw configuration of this new lizard is so closely similar to Eumeces-like scincids that I cannot consider the similarity as

convergent. From current understanding of scincoid evolution, the slenderness and the dorsal curvature of the subdental shelf anteriorly are likely more derived character states than the stronger and straight subdental shelf in Recent gerrhosaurine cordylids. Accordingly, if Orthrioscincus is a primitive gerrhosaur, it would be difficult to explain why such an early member of the group (Judithian in age) has such a derived morphology in the dentary.

2) Orthrioscincus may be a primitive member of the Scincidae that is broadly related to the Recent Eumeces group. In this interpretation, the similar jaw configuration, especially its slenderness and the curvature of the subdental shelf, is the guide to relationship; in that case, the similarity in cusp pattern to Gerrhosaurus indicates a similar type of food preference. According to Mattison (1989: 164), Recent Gerrhosaurus lizards "eat a substantial amount of plant material, but are otherwise insectivorous."

Nevertheless, Orthrioscincus is a Judithian member of the Scincoidea, as it shows a mosaic of a Eumeces-like dentary structure and Gerrhosaurus-like teeth. Here I tentatively place this genus in the family Scincidae, regarding the similarity in dentary structure as a reliable indication of relationship, and the Gerrhosaurus-like crown pattern as convergent. The evolutionary history of the Scincoidea is poorly known, because both the Scincidae and the Cordylidae have a poor fossil record. Before this study, the earliest fossil genus known for the Scincoidea was Sauriscus Estes 1964 from the Lance Formation, eastern Wyoming, while another genus, Contogenys, known from the same horizon is probably not a scincoid (see discussion about Contogenys below). The newly discovered specimens described here are hence significant for understanding the early evolution of the Scincoidea (see general discussion on the evolution of Late Cretaceous lizards in western Canada in last section).

Genus *Aocnodromeus* n. gen.

Type species: *Aocnodromeus corrugatus* n. sp..

Range: Upper Cretaceous, North America.

Diagnosis: As for the type and only known species.

Etymology: *aoknos* + *dromeus* (Gr., m.), meaning restless runner.

Aocnodromeus corrugatus n. sp.

Plate 9, Figs. 7-10; Text-fig. 19

Holotype: UALVP 29905, a nearly complete left dentary bearing 11 teeth and spaces for five others.

Type locality and horizon: MR-6 locality, Verdigris Coulee, approximately 30 km east of the Village of Milk River, southern Alberta; upper member of the Milk River Formation (Aquilan in age).

Referred specimen: UALVP 29906, left dentary fragment with nine anterior tooth positions.

Known distribution: Currently known only from the type locality.

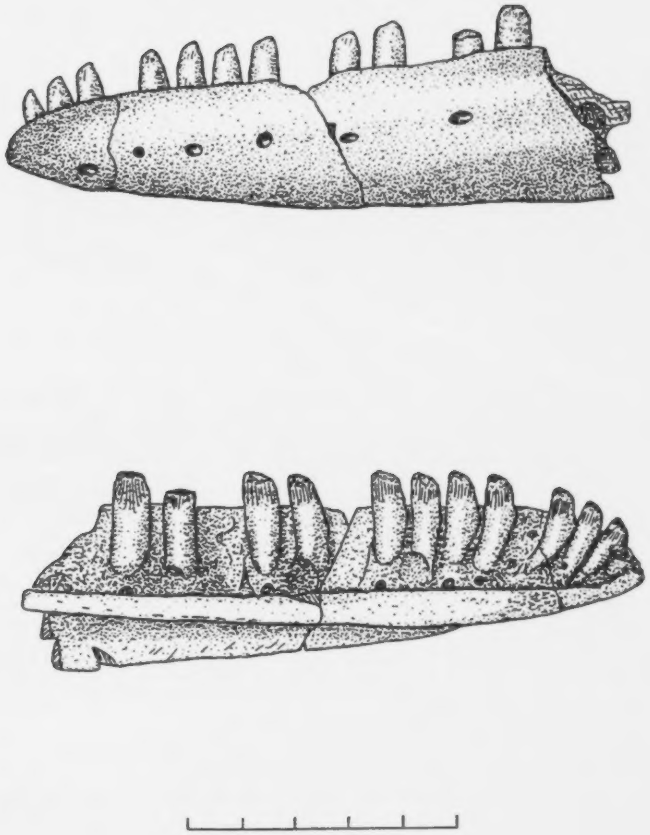
Diagnosis: Aquilan scincomorphan lizard charaterized by having the following combination of character states: dentary heavily built, having robust subdental shelf and well-defined sulcus dentalis; dentary teeth solidly subcolumnar, widely spaced, having heavy basal cementum; tooth crowns obtusely unicuspid, medially concave and striated; posterior teeth molariform, with laterally compressed and somewhat squared off crowns.

Etymology: corrugatus (L.), meaning wrinkled, in reference to the wrinkled enamel on the tooth crown of this lizard.

Description: The holotype (UALVP 29905) is well preserved, showing most of the dentary and 16 tooth positions. The dentary is broken posteriorly at the 16th tooth position, but with no evidence of the posterior interior alveolar foramen that opens close to the posterior end of the tooth row. The proportions of the dentary indicate that the jaw was shallow, elongated, but quite robustly built.

In medial view, the dentary shows a straight and robust subdental shelf, which gently decreases its depth posteriorly. The maximum depth of the shelf is slightly less than the half of the tooth height. Dorsally on the shelf is a well-defined sulcus dentalis medial to the tooth row; the sulcus lacks a sharp dorsal ridge for its medial border. Below the subdental shelf, the Meckelian canal is restricted; its maximum depth is shallower than the lateral parapet of dentary. Posteriorly, the depth and width of the canal are about equal, and the canal is roughly triangle in cross-section. The restricted Meckelian canal indicates that the splenial (not preserved) was probably narrow and elongated, and the splenodentary articulation terminated anteriorly below the seventh and the eighth teeth from the front.

The dentary teeth are widely spaced from one another and are pleurodont, with about two-thirds of their height attaching to the lateral parapet of the dentary. The tooth shafts are solidly built and subcolumnar; even the anteriormost ones show little anteroposterior compression. Each tooth has a small foramen at the tooth base, while at least three (the 8th, the 11th, and the 14th) have developed a basal excavation medioposteriorly of the tooth base for the replacing tooth. The posteromedial location of these basal excavations indicates an "intermediate method" (Edmund 1969) of tooth replacement for this lizard. All of the dentary teeth that are preserved have their bases heavily cemented to the dentary. The tooth crowns are medially concave and striated, but labially smooth. The anterior and middle teeth



Text-fig. 19. Scincidae, Aocnodromeus corrugatus n. gen. et sp., upper member of Milk River Formation, southern Alberta; UALVP 29905 (holotype), incomplete right dentary; (above) lateral view, (below) medial view. Scale = 5 mm.

(the first 14 on this specimen) are unicuspid, with the tooth apex curved posteromedially to form "an inwardly pointing V" (Estes 1964: 125) in dorsal view; but the crowns of the posterior teeth (the last five to seven) tend to be lingolabially compressed, and more or less truncate. The lingual striations on these posterior teeth are also stronger than those on the anterior and middle teeth. This difference in crown pattern of the posterior teeth is clearly shown on the completely preserved 15th tooth on the holotype.

The lateral surface of the dentary is smooth, and gently convex both dorsoventrally and anteroposteriorly. This surface shows six small and round inferior alveolar foramina that are widely spaced, with the space between them increasing gradually posteriorly. The last foramen on the specimen is located lateral to the 14th tooth position.

Discussion: From the characters described above, the specimen UALVP 29905 from the upper member of the Milk River Formation represents a new genus and new species that can be placed in Scincomorpha; it shows a well-defined subdental shelf and a sulcus dentalis, and no indication of a vertically directed intramandibular septum. The familial affinities of this lizard are difficult to determine, because there is no reliable character state (synapomorphy at the familial level) shown on the UALVP 29905 (the coronoid, an important structure, is broken off). The tooth form of this lizard (unicuspid crowns curved to form an "inwardly pointing V," medial striations, and small basal foramen) indicates possible affinity to the family Scincidae (broadly resembling the Mabuya subgroup in these features). But the robustness of the dentary and strong mandibular symphysis, especially the robust subdental shelf, are equally indicative of cordylid affinities. This new lizard is tentatively referred to the Scincidae, pending further study on more specimens to clarify its taxonomic affiliation.

Estes et al. (1988: 226) cited Gauthier's (1982) recognition of medial striations on the tooth crowns as an anguid synapomorphy; in fact, Gauthier's (1982: 19) original statement cited the combination of the "teeth with twisted, chisel-shaped, striated, unicuspid and obtusely-pointed crowns" as the synapomorphy. Nevertheless, it might be worthwhile to point out here that the presence of medial striations on the tooth crowns also occurs in several scincomorphan families: Scincidae (e.g., Eumeces), Cordylidae (e.g., Cordylus), and in Xantusiidae (e.g., Palaeoxantusia). Presence of this character in the early scincoid Aocnodromeus, corroborated with other evidence from Cretaceous fossil scincomorphans, suggests that this character is symplesiomorphic for scincomorphans. Of course, the medial striations in Anguidae, especially in glyptosaurines, are much stronger than those in the other groups, and are frequently associated with an obtuse, chisel-shaped cutting edge of the crown. The latter combination is obviously best designed for plant-eating, functionally different seemingly from that in insectivorous or omnivorous scincids and others. Whether the presence of medial striations in the Anguidae is homologous to that in scincomorphans is still an open question.

The "inwardly-pointing V" crown pattern recognized by Estes (1964) in some anguids is comparable to the problem concerning the medial striations: this morphology also occurs in some scincids, particularly those in the Mabuya group. The occurrence of a similar crown pattern in the two phylogenetically remote groups is probably correlated with a similar food preference, and is thus convergent; it can be easily distinguished from one another in reference to other characters, such as jaw construction. Estes et al. (1988) argued that this kind of similarity does not invalidate the synapomorphic status of the "inwardly-pointing V" crown pattern for the Anguidae, because the "inwardly-pointing V" in the Anguidae and that in the Scincidae are not the same character in terms of origin, although they are the same in terms of morphology.

Family ?Cordylidae Gray 1837

Genus & species undetermined (A)

Plate 10, Figs. 1-2

Specimens: UALVP 29810, fragmentary dentary with 12 tooth positions (four teeth plus the bases and spaces of eight others); UALVP 29907, fragmentary dentary with the bases and spaces for ten teeth.

Locality and horizon: Outcrop of the Oldman Formation near Irvine, in Sec. 31, Tp. 11, R 2, W 4, about 40 km east of Medicine Hat, southeastern Alberta; Upper Cretaceous Oldman Formation (Judithian in age).

Description: Of the two specimens above, UALVP 29810 is the better preserved, having four teeth in place, while those on UALVP 29907 are all broken off. What remains of the dentary of UALVP 29810 is short and robust; and the dentary is broken at the twelfth tooth position, so that its posterior end, especially the taxonomically important coronoid process, is unpreserved.

The dentary bears a robust subdental shelf, the maximum depth of which is about half of the tooth height. The depth and the robustness of the shelf remain unchanged below the first eight tooth positions, but the shelf is reduced posteriorly from below the ninth position, where the anterodorsal splenodentary articulation terminates (judging from the articulatory scar on the specimen) and the Meckelian canal becomes deeper and faces more medially. The subdental shelf dorsally bears a shallow but clearly defined sulcus dentalis, along the medial side of the tooth row.

Among the four teeth preserved on UALVP 29810, two (the sixth and the eighth) are complete, and the other two (the fourth and the fifth) have the bases and the shafts preserved but the crowns are broken off. The teeth are pleurodont, with the upper one-third of the tooth height projecting above the lateral parapet of the dentary. The tooth shafts, closely spaced along the tooth row, are strongly compressed anteroposteriorly, but lack a shoulder-like medial expansion. Both of the two complete teeth on the jaw have developed a resorption cavity at the tooth base, and in another tooth (the fifth), the lower half of the tooth has been resorbed. These indicate that the tooth replacement of this lizard is likely direct or by the so-called "iguanid method" (Edmund 1969), which is also seen in Recent cordylids (ibid.).

The tooth crowns are unicuspid with a blunt, inwardly curved cusp and clearly defined anterior and posterior vertical ridges. The crowns show no indication of lateral compression, no tendency toward becoming chisel-like, and lack striae on both the medial and lateral surfaces.

The lateral surface of the dentary is smooth, slightly convex, and has small inferior alveolar foramina that are unevenly spaced from one another. The posterior foramina tend to be closer to the upper rim of the jaw.

The second specimen (UALVP 29907) shows the same general proportions as UALVP 29810, but obviously is more slender in correspondence with its smaller size. The teeth are all broken off, but the tooth bases clearly show that these teeth were strongly compressed anteroposteriorly, and were closely packed along the tooth row, as in UALVP 29810. This specimen shows that the posterior interior alveolar foramen opens into the Meckelian canal close to the posterior end of the tooth row, but there is no indication of a vertically directed intramandibular septum.

Discussion: The two specimens described above represent a previously unknown fossil scincomorphan taxon. This taxon remains unnamed in this paper, because the two specimens are not complete enough to provide an adequate diagnosis of a new genus and species. The familial assignment of this lizard is difficult from the evidence at hand; however, the shape of the dentary and the tooth form suggest possible affinities with the family Cordylidae. The dentary is closely similar to that of Saurillodon Estes 1983a, an Upper Jurassic scincomorphan from Portugal that Seiffert (1973) put in the Scincidae but Estes (1983a) put in the Paramacellodidae Estes 1983a. In both the dentary is short, with a low number of teeth and a characteristically robust subdental shelf. However, the new lizard from the Oldman Formation can not be assigned to Saurillodon, not only because of differences in geological age and geographical distribution, but more importantly in tooth form: Saurillodon has conical teeth with columnar shafts, while the compressed shaft, obtuse crown, and lateral ridges on the teeth in the new lizard resemble corresponding parts of the teeth of Recent Cordylus. The family Paramacellodidae, as a primitive group, is closely related to the Cordylidae, and may be a possible synonym of the latter (Estes 1983a).

The similar proportions of the dentary of the Oldman species and the Jurassic Saurillodon could be regarded as a primitive character for cordylids, but the similarity to Cordylus in morphology of the teeth is probably more indicative of its familial affinity. Other evidence, concerning the splenial, supports this interpretation: although the splenial is not preserved on both UALVP 29810 and 29907, a scar shows that the dorsal splenodentary articulation terminated anteriorly close to the midpoint of the tooth row. Similar proportions are seen in Recent Cordylus (pers. observ.), while Jurassic Saurillodon shows a more anterior, presumably primitive, extension of the splenial.

Genus & species undetermined (B)

Plate 10, Fig. 3

Specimen: UALVP 29722, incomplete left dentary having seven teeth and the base as well as the spaces of four others.

Locality and horizon: Bug Creek Anthills, McCone County, Montana; Upper Cretaceous Hell Creek Formation (Lancian in age).

Description: UALVP 29722 is a short, shallow, and lightly built left dentary with 11 tooth positions preserved. The anterior end of the bone is slightly rounded by erosion, with probably only the first tooth position missing. The dentary is posteriorly broken close to the posterior end of tooth row, as the subdental shelf is greatly diminished corresponding to the termination of the tooth row.

In medial view, the subdental shelf is anteriorly deep and robust below the first six teeth, but abruptly reduced posteriorly from the seventh tooth position. The maximum depth of the shelf anteriorly is about half of the tooth height. The ventral edge of the shelf has a shallow but clearly defined groove for the dorsal splenodentary articulation, and this groove terminates anteriorly below the seventh tooth position. The Meckelian canal below the subdental shelf is extremely narrow and open ventrally below the first seven teeth, but is greatly deepened posteriorly with the posteriorly diminishing subdental shelf. The maximum depth of the canal at its posterior end slightly exceeds the height of the lateral parapet of dentary. The sulcus dentalis is so poorly developed that it is barely recognizable.

The dentary retains seven teeth, and the tooth bases of four others, in total, representing the second through the twelfth positions on the dentary tooth row. Most of the teeth have the crowns broken off, but the eleventh tooth (the only well-preserved tooth on the specimen) clearly shows a blunt, almost rounded central cusp, and faintly developed side cusps. The first three teeth are slightly compressed anteroposteriorly; the remainder are generally pillar-like, with a narrow crown but thickened shaft. Several broken teeth show a round cross-section, with a thick tooth wall and thin tube-like pulp cavity. A basal deposit of cementum can be seen around the tooth bases, but this is far less than seen in teiids. On this specimen, only the third tooth has a basal excavation for a replacing tooth at the medial side of the tooth bases; the rest show no sign of replacement pits. The teeth are pleurodont, having the lower half or more of the teeth attached to the lateral parapet of the jaw.

The lateral surface of the dentary is smooth, and is gently convex. Unlike UALVP 29810 (genus & species undetermined A) described above, this specimen has only three small inferior alveolar foramina shown on the lateral surface of the jaw, and these foramina are widely spaced from each other.

Discussion: The specimen UALVP 29722 from the Hell Creek Formation represents a lizard that may be closely related to "genus & species undetermined A" from the Oldman Formation (UALVP 29810); for this reason, this Hell Creek specimen is included in this study. These two lizards, although from two geologic formations, share close similarities in the configuration of the dentary (short dentary, robust subdental shelf, and extremely narrow Meckelian canal) and the mode of tooth attachment, but the Hell Creek form B differs from the Oldman form A in having cylindrical tooth shafts, incipiently tricuspid tooth crowns, and poor development of sulcus dentalis. The morphologic differences between the two lizards (corroborated with their geologic ages) indicate that they may pertain, at least, to two different species.

Family ?Xantusiidae Baird 1859

Genus & species new (unnamed)

Plate 10, Fig. 4

Specimen: UALVP 29840, fragmentary right mandible consists of partially fused splenodentary bearing six teeth and the tooth bases for three others.

Locality and horizon: Bug Creek Anthills, McCone County, Montana; Upper Cretaceous Hell Creek Formation (Lancian in age).

Description: The specimen UALVP 29840 is a small right splenodentary having nine tooth positions preserved. Although incomplete, the dentary is short, probably bearing no more than 15 teeth originally. In medial view, the well-defined subdental shelf is at such a low position (similar to that in Contogenys Estes 1969b) that the Meckelian canal is extremely restricted dorsoventrally. In cross-section, exposed posteriorly where the dentary is broken, the Meckelian canal is just slightly wider than the more laterally located mental canal (inferior alveolar canal). The splenial is greatly narrowed, but not retracted posteriorly, is medioventrally located, and partially fused to the dentary along the ventral splenodentary articulation below the anterior inferior alveolar foramen, which penetrates the splenial below probably the fourth or the fifth tooth position from the rear.

Although the general proportions of this specimen are similar to those of the dentary of Contogenys, the teeth are obviously different. The preserved part of the dentary bears nine tooth positions, including six teeth and the tooth bases for three others. These teeth are so closely spaced along the tooth row that actually little free space intervenes between successive teeth. The tooth attachment is pleurodont, with one-third of the tooth height projecting above the lateral parapet of dentary. The tooth shafts are cylindrical, lacking either anteroposterior compression or medial expansion. The tooth crowns are non-striated, and are bluntly conical with faint anterior and posterior lateral ridges. Two teeth on the jaw have developed deep resorption pits medially at the base, suggesting possible direct replacement (Rieppel 1978) or the "iguanid method" of tooth replacement (Edmund 1969), in which the replacement teeth are developed directly at the bases of old teeth (ibid.).

The lateral surface of the jaw is smooth, and shows three tiny lateral inferior alveolar foramina that are equally spaced from one another. The ventral border of the dentary is strongly turned medially, so that the ventral splenodentary articulation (partially fused) is entirely medial to the ventral midline of the jaw.

Discussion: The specimen UALVP 29840 from the Hell Creek Formation represents a previously unknown lizard, which may be closely related to a Contogenys-like form occurring in the study area (see later discussion), and for this reason, this new specimen is included in this study. In terms of dentary structure and tooth morphology, the new lizard from the Hell Creek Formation is characterized by a combination of character states, including: a short splenodentary having the splenial greatly narrowed and partially fused to the dentary; a strong tendency to enclose the dentary tube by splenodentary fusion; and pleurodont dentary teeth having cylindrical shafts, with conical and non-striated crowns. However, the new lizard is only known from a single specimen that is not complete enough to be a name-bearer of a new species; therefore, it is appropriate to leave the new genus and species unnamed until more, better preserved specimens are found.

The specimen UALVP 29840 shows a strong subdental shelf, a well-defined sulcus dentalis, and an indication of direct tooth replacement. These together are indicative of a scincomorphan relationship for this lizard. However, the familial affinities of this species are somewhat uncertain, as the splenodentary is too incomplete to show reliable synapomorphies with a scincomorphan family. Both the shape of the dentary and the tooth form of this species show close similarities to those of Palaeoxantusia Hecht 1956 (see discussion below), indicating a possible affinity with the family Xantusiidae. The partial fusion with the dentary of the greatly narrowed splenial shows a tendency to develop an enclosed dentary tube, which is characteristic for the Xantusiidae (see Estes et al. 1988). On the basis of these similarities, I tentatively classify this species in the Xantusiidae, until further study on more complete specimens can clarify its taxonomic position.

The lizard Palaeoxantusia was originally named by Hecht (1956: 4) as an Eocene "xantusiid lizard distinguished from the smaller members of the genus Xantusia by its smaller size, more robust dentary, its distinct splenio-dentary depression, and groove for the adductor mandibulae externus superficialis." At present, the genus has four species and a geologic range from middle Paleocene to lower Oligocene (see Schatzinger 1975a-b, 1980; Estes 1983a: 123). The type species Palaeoxantusia fera (Hecht 1956) was founded on an almost complete splenodentary (holotype AMNH 3815) from middle Eocene beds, at the west end of Elk Mountain, Sublette County, Wyoming. The splenodentary is short and robust, with 13 tooth positions. "The teeth are pleurodont, conical, robust, and rounded at the apex. Below the teeth on the internal surface there is a distinct shelf with a groove" (Hecht 1956: 5).

The specimen UALVP 29840 from the Hell Creek Formation shows great similarity in jaw construction and tooth form to the above-mentioned lizard, indicating its close relationship to the Tertiary Palaeoxantusia. However, UALVP 20840 differs from the splenodentary of Tertiary Palaeoxantusia in having a comparatively larger splenial that is less extensively fused to the dentary, and in having the Meckelian canal open anteriorly. The currently known fossil evidence of Palaeoxantusia indicates that these are primitive character states. According to Savage (1963), Palaeoxantusia is more primitive than Xantusia Baird 1859 in morphology of the splenodentary, and may represent the ancestral stock from which the latter form is derived.

From the available evidence, the Hell Creek specimen is geologically older, and structurally more primitive than Palaeoxantusia. The ventral splenodentary articulation below the anterior inferior alveolar foramen is clearly fused without a suture, and this fusion can be regarded as the initial step from a more generalized form towards the complete fusion of splenodentary and the enclosure of the dentary tube in early evolution of the Xantusiidae. Therefore, UALVP 29840 may represent a structural ancestor of the later Palaeoxantusia, from which the more recent Xantusia and its closely related forms are derived.

Another Late Cretaceous lizard, Contogenys Estes 1969b, was tentatively placed in the family Scincidae previously (Estes 1969b, 1983a); but it is removed from that family in this study (see following discussion). The results of this study also suggest that Contogenys may be in some degree related to the Xantusia lineage, while being less closely related to Palaeoxantusia than the unnamed new lizard described above.

Genus *Contogenys* Estes 1969b, n. emend., removed from family Scincidae.

Type species: *Contogenys sloani* Estes 1969b.

Range: Upper Cretaceous, North America.

Diagnosis: As for the type species.

Contogenys sloani Estes 1969b, n. emend., excl. specs. YPM-PU 17035, 17036a-b (Estes' referred specimens).

Plate 10; Figs.5-6

Holotype: MCZ 3681, nearly complete left dentary having five teeth and the spaces for ten others (see Estes 1969b).

Paratypes: MCZ 3682-3685, fragmentary maxillary and dentaries (Estes 1969b).

Type locality and horizon: BCA locality, SW 1/4, Sec. 9, Tp. 22, R 43, McCone County, Montana; Upper Cretaceous Hell Creek Formation (Lancian in age).

Included specimen: UALVP 29839, topotypic right dentary collected by a UALVP field party in 1969. This specimen is included in here because it provides new information for a taxonomic revision of *Contogenys sloani*, which appears to be phyletically close to an undetermined taxon from the study area (family incertae sedis, genus & species undetermined, see p. 164).

Known distribution: Upper Cretaceous Hell Creek Formation, eastern Montana. The referrals of several Paleocene specimens (YPM-PU and AMNH specimens) to this taxon are unconvincing (see later discussion). There is also a recent report of the specimens of this genus from the Judithian beds of New Jersey (Denton et al. 1991), but detailed taxonomic description is as yet unpublished.

Diagnosis (revised from Estes 1983a): A scincomorphan lizard characterized by the following combination of character states: dentary short, with 16 or fewer teeth; tooth shafts anteroposteriorly compressed, and medially expanded; tooth crowns truncate, having weak anteroposterior apical groove flanked by crests; inferior alveolar canal distinctly wider than Meckelian canal.

Description: Estes (1969b) has provided a sufficient description of the holotype (MCZ 3681) and the several Paleocene specimens. However, the newly collected topotypic specimen (UALVP 29839) reveals new information and provides the basis for the emendation of this taxon. Therefore, a description of the new specimen is neccesary, in comparison with the original description of the holotype.

The specimen UALVP 29839 has only the anterior tip and the posteroventral corner missing; otherwise it is complete. Like the holotype, the newly discovered dentary is extremely short and relatively deep, having 15 tooth positions in the complete tooth row, including three complete teeth, bases for two more, and spaces for ten others. In medial view, the subdental shelf is at a position close to the ventral margin of the jaw; the ventral position of the shelf, combined with the widening of the inferior alveolar canal results in a greatly restricted Meckelian canal, which forms an extremely narrow tube. The intramandibular septum is vertically directed, but has no free ventral border differing from that in anguimorphans). The splenial, which is firmly articulated with the dentary, is greatly reduced dorsoventrally and terminates anteriorly below the sixth tooth position. The anterior inferior alveolar foramen penetrates the splenial below the fourth posteriormost tooth.

The subdental shelf curves posterodorsally, ending at the last dentary tooth; immediately behind this tooth and medial to the small but prominent coronoid process of dentary is a distinct facet that received the anteromedial process of the coronoid bone (Estes 1969b), which is not preserved. The subdental shelf lacks a dorsal ridge, and the sulcus dentalis is poorly defined (contrary to Estes 1969b). The dentary teeth are pleurodont, having one-third of their height projecting above the high lateral parapet of dentary. The tooth shafts are strongly compressed anteroposteriorly, with a weakly developed, shoulder-like, medial expansion. Small replacement pits that open medially are clearly shown at the tooth bases. The tooth crowns are squared-off, more or less chisel-like, with slight lateral compression. There are no medial striations, but faint anterior and posterior ridges are developed.

The lateral surface of the dentary is strongly convex, reflecting the wide inferior alveolar canal internally, which is wider than the greatly reduced Meckelian canal in posterior view. Posterolateral and below the small coronoid process of dentary is a distinct depression for the attachment of adductor muscle (Estes 1969b). The posteroventral part of the dentary is broken off, but clearly shows a large base for the ventroposterior process. The lateral surface of the dentary has a row of inferior alveolar foramina as commonly seen in other lizards, but as a minor individual variant, at least two extra foramina are developed anteriorly below the main row (the holotype MCZ 3681 shows a similar condition, see Estes 1969b, fig. 1a).

Discussion: Estes (1969b) founded Contogenys sloani on several specimens (maxillary, dentary, and parietal materials) from the BCA locality, and assigned the species to the family Scincidae. In the same paper, he also referred several specimens (YPM-PU 17035, 17036a-b) from the Paleocene Tongue River Formation, Montana, to this species (see Estes 1969b). The results of this study show that both the classification of Contogenys in the

Scincidae and the referral of the Paleocene YPM-PU specimens to this species are questionable. Sullivan (1982) referred a maxillary from the "Fort Union Formation" to this species, but as discussed below, this referral is highly questionable as well, as it is based on an invalid character.

1) Familial Classification of Contogenys

The original classification of Contogenys in the Scincidae was largely "on the basis of the Eumeces-like wedge on the posterior border of the maxilla and on the general appearance of the teeth" (Estes 1969b: 5). However, the following observations indicate that the character states on which this placement is based are incorrect: (1) The maxillary of Eumeces (also that of Mabuya) has an anteriorly pointing triangular notch between dorsal and ventral posteriorly directed processes; the dorsal process fits in a triangular depression on the lateral surface of the jugal, so that the maxillary-jugal suture is actually Z-shaped in lateral view (pers. observ.). Therefore, Estes' (1969b) "triangular wedge inserted into the jugal" is an inacurate statement. (2) The "triangular wedge" on MCZ 3682 (maxillary) seems not to be original but a result of breakage of its ventral edge, as no known lizards have a jugal that is wide enough to accept such a robust "triangular wedge." (3) Contogenys has a short jaw with fewer, more or less chisel-shaped teeth, showing no resemblance to Recent scincids (e.g., Eumeces and Mabuya), which have elongated jaws with numerous unicuspid teeth. Therefore, Estes' (1983b: 370) "Eumeces-like aspect" of Contogenys is incorrect, and cannot be used to support referral of this lizard to the Scincidae.

In this study, I have compared Contogenys with the early Tertiary Paleoxantusia (see Hecht 1956; Estes 1983a); similarities between the two may suggest a relationship that Contogenys is a xantusiid. The general jaw configuration and the tooth form of the two lizards are closely similar. They both have a short dentary with relatively few, more or less chisel-shaped teeth, each with a small basal foramen, and a small, but prominent, coronoid process of the dentary with a distinct posterodorsal facet (see Estes 1983a, fig. 31B). In both

Contogenys and Palaeoxantusia, the dentary has a large ventroposterior process (or Meckelian process [Estes 1969b]) that extends posteriorly well beyond the dorsal coronoid process of the mandible. This condition is in contrast with that of scincids, in which the two processes are more or less equally developed, but is unique (synapomorphic) to the Xantusiidae (pers. observ.). This condition is also seen in Eoxanta Borsuk-Bialynicka 1988, a possible early xantusiid from the Upper Cretaceous of the Gobi Desert (Borsuk-Bialynicka 1988). The only notable difference in dentary construction between Contogenys and Palaeoxantusia is the enclosed dentary tube in the latter; however, its Cretaceous relative might be expected to have an unfused dentary tube, but one showing the tendency towards fusion, as is the case with Contogenys. Furthermore, MCZ 3682 a paratype of Contogenys (see Estes 1969b, fig. 2; 1983a, fig. 26D), shows a distinct ventrally directed curvature at the posterior end of the supradental shelf. A similar condition is seen in Recent Xantusia, but not in Eumeces or Mabuya (pers. observ.). This adds another character state indicating the affinity of Contogenys to the Xantusiidae, not to the Scincidae.

The holotype (MCZ 3681) and the new specimen described above also show some anguid-like features: the anterior part of the Meckelian canal is open ventrally, and the teeth are more or less chisel-shaped; however, the well-developed coronoid process of the dentary and the absence of a vertically directed intramandibular septum with a free ventral border strongly suggest a scincomorphan relationship (see Estes et al. 1988 for list of scincomorphan synapomorphies). Thus, the similarities to anguids are evidently convergent.

As indicated in the above discussion, I have found no solid evidence indicating that Contogenys is a member of the family Scincidae, but have noted some resemblances to Palaeoxantusia and Xantusia. I believe that an enlarged posteroventral process of dentary and a posteroventral curvature of supradental shelf are synapomorphic for a taxon that includes Recent Xantusia, fossil Palaeoxantusia and Contogenys (if they are not in the same family). Therefore, Contogenys is tentatively placed in the Xantusiidae in this paper, pending verification by a more extensive study of fossil and Recent materials.

2) Problem with the Referral of Several Paleocene Specimens

The YPM-PU specimens referred to *Contogenys sloani* by Estes (1969b) include several dentaries from the mid-Paleocene Tongue River Formation, Montana. These specimens, as Estes (1969b, fig. 4) figured, differ from the holotype (MCZ 3681) and other Late Cretaceous specimens of *Contogenys* in having columnar teeth, a more prominent subdental shelf, and a much wider Meckelian canal, indicating a larger splenial. All of these differences are beyond the range of individual variation from current understanding of other fossil and living lizard species. The short jaw with fewer teeth and the nature of the coronoid process of the dentary may suggest an affinity with *Contogenys* at or above the generic level, but these specimens do not belong to *C. sloani*. Therefore, the YPM-PU specimens from the mid-Paleocene Tongue River Formation should be removed from *C. sloani*; a restudy of these specimens is needed.

Sullivan (1982) identified AMNH 12069 (from the mid-Paleocene "Fort Union Formation," Wyoming) as a right maxillary, and referred it to "cf. *Contogenys sloani*," which Estes later (1983a) listed as "cf. *Contogenys* sp.." According to Sullivan (1982: 999), the referral of this specimen to *Contogenys sloani* is "on the evidence of an expansion of the maxilla posterolaterally that indicates the probable presence of a triangular wedge (as reported by Estes, 1969) as well as the presence of strongly pleurodont teeth with squared-off tooth crowns." As discussed before, the so-called "trianguiar wedge" is not a diagnostic feature for *Contogenys*, nor for the Scincidae. Another feature on which Sullivan's referral is based, "strongly pleurodont teeth with squared-off tooth crowns," is not unique to *Contogenys*, but shared with many other lizard taxa in Xantusiidae, Anguidae, and several other families. Sullivan's (1982, text-fig. 4) figure shows that the teeth on AMNH 12069 are not strongly anteroposteriorly compressed and lack a basal foramen, well-developed in *Contogenys sloani* (see Estes 1969b, figs. 1-2). The figure also shows that AMNH 12069 is possibly a left maxillary rather than right, the teeth are often slightly recurved, not curved forward. The fragmentary nature of the specimen makes further comments difficult; however, it seems to me that the specimen is, in both size and tooth morphology, indistinguishable from Palaeoxantusia from the same locality.

3) The Status of Paracontogenys Schatzinger 1975a in Golz & Lillegraven 1977

Schatzinger (1975a) founded Paracontogenys estesi on several specimens from the upper Eocene Mission Valley Formation, San Diego, California. This lizard is diagnosed as an Eocene scincid differing from Contogenys in having a greater number of dentary teeth, a closed Meckelian canal, and medial striations on tooth crowns (Schatzinger 1975a; also see Estes 1983a). As Schatzinger (1975a) noted, this Eocene lizard is closely similar to the Late Cretaceous Contogenys; however, as is the case with Contogenys, its familial placement in the Scincidae is questionable, as no diagnostic characters for Scincidae are shown on the specimens; like Contogenys, it may pertain to the Xantusiidae.

Probably regarding the faint medial striations on the tooth crowns as a systematically significant character, Estes (1983a: 111) commented that "a reference [of Paracontogenys] to Xantusiidae is possible but improbable as tooth crown structure is more like scincids than xantusiids." Now it is clear that this character is also seen in other scincomorphan families, including primitive Xantusiidae; it also convergently occurs in Anguidae, especially in glyptosaurines (see, e.g., Gauthier 1982). It should be pointed out that the occurrence of similar striations in Jurassic paramacellodids (see Estes 1983a) suggest that this character probably is symplesiomorphic for scincomorphans, but is not a diagnostic character for the Scincidae. It seems to me that Paracontogenys is best be referred to the Xantusiidae. The most indicative character of Paracontogenys in respect to its familial affinities is probably its extensive fusion of the dentary tube accompanied by a great reduction (or total loss) of the splenial. A short jaw, with the fusion of dentary tube extending posteriorly close to the posterior end of tooth row, is characteristically the xantusiid condition, which is different from that of the Scincidae, in which the dentary is elongate and only the anterior half of the tube is closed with the posterior half covered by the splenial (pers. observ.).

Above all, it is suggested by the fossil evidence that Contogenys and Paracontogenys are not members of the Scincidae. I classify them as "family incertae sedis," although I strongly believe that their affinities are with the Xantusiidae. An incomplete survey of dentary struture indicates that the following character states are possibly synapomorphic for the Xantusiidae: (1) ventroposterior process (or Meckelian process) of the dentary is larger than the coronoid process of dentary; (2) ventroposterior process of dentary extends posteriorly well beyond the summit of the dorsal coronoid process; (3) coronoid process of the dentary medially has a distinct facet behind tooth row (Hecht 1956). The first two character states are convergent in Pygopodidae (see Estes et al. 1988, fig. 20), while the third character state is unambigiuously unique for the Xantusiidae.

Family incertae sedis

Genus & species new (A)

Plate 11, Fig. 1

Specimen: SMNH P1927.880, incomplete right dentary bearing eight well-preserved teeth and the broken bases of two others.

Locality and horizon: Gryde locality, in Sec. 19, Tp. 4, R. 18, W. 3, Frenchman River Valley, southwestern Saskatchewan; Upper Cretaceous Frenchman Formation (Lancian in age).

Description: The specimen SMNH P1927.880 is the anterior half of a right dentary, which is broken immediately behind the tenth tooth, and also posteroventrally at the Meckelian canal. The specimen shows no indication of erosion through transportation, but displays several tooth marks, probably from a sharp-toothed predatory lizard or a small mammal.

Medially, the dentary bears a robust subdental shelf, which is anteriorly as deep as the height of the teeth but sharply diminishes posteriorly. The mandibular symphysis is strong, with a robust symphysial process; its articulating surface faces ventromedially. The subdental shelf bears a sharp dorsal ridge, which medially borders a narrow and deep sulcus dentalis along the tooth row. The Meckelian canal is greatly narrowed anteriorly, to a fissure-like opening under the first four tooth positions; it is widely open posteriorly, correponding to the deepening of the jaw and the diminishing of the subdental shelf. The widely opened Meckelian canal on this specimen clearly indicates an extensive splenial.

The specimen shows eight well-preserved teeth and the broken bases of two others, representing the first ten tooth positions of the complete dentary tooth row. The teeth are pleurodont, having about half of the tooth height projecting above the lateral parapet of the dentary. Most of the teeth show a deep basal excavation, with part of the tooth base already having been resorbed. This type of basal excavation obviously indicates direct tooth replacement (Edmund 1969). The tooth shafts are anteroposteriorly compressed for the first three or four teeth, but increasingly become pillar-like toward the posterior end of the tooth row. The tooth crowns are bluntly conical, with a weak crest (or ridge) encircling the crown surface. The medial surface of the crown is faintly striated.

The lateral view of the specimen clearly shows that the dentary is more or less wedge-shaped, having the horizontal dorsal border diverging posteriorly from the ventral border at the angle of 40-45 degrees. This particular jaw configuration to some extent resembles that of some Jurassic paramacellodids (e.g., Becklesius, see Estes 1983a, fig. 28-I). The lateral surface of the dentary shows five inferior alveolar foramina that are small and rounded. The first four are equally spaced from one another, but the fifth is separated from the fourth by a space twice the length of those between the more anterior foramina.

Discussion: As described above, SMNH P1927.880 shows a well-developed subdental shelf and sulcus dentalis, and a widely open Meckelian canal indicating an extensive splenial. On the basis of these characters, this lizard can be confidently placed in the infraorder Scincomorpha; however, its familial relationships cannot be determined at present, because no clearly synapomorphic character states can be recognized on this specimen. Nevertheless, this new Lancian lizard differs from members of the Teiidae (one of the most common North American Late Cretaceous scincomorphan groups) in having a less heavy deposit of basal cementum and a different tooth replacement pattern, as shown by the deeply excavated pits (compared to subcircular replacement pits in teiids). Instead, both the general jaw construction and the tooth form of this new lizard closely resemble those of Becklesius hoffstetteri (see Estes 1983a, fig. 28), which is currently classified in the family

Paramacellodidae (Estes 1983a). Paramacellodids are known only from the Upper Jurassic of Europe, particularly from England and Portugal. "At present the family has utility only in segregating some Jurassic forms that on present material cannot be referred to the Holocene family [Cordylidae] owing to lack of knowledge of the temporal region" (Estes 1983a: 115). Both the geologic (Upper Jurassic) and geographic (Europe) distributions of paramacellodids seem to prevent the referral of this species to the European Jurassic family. However, the above-mentioned similarities indeed shed some light on its possible affinity to the family Cordylidae, since the close relationship of Paramacellodidae with Cordylidae has been suggested by resemblances in mandibular construction and osteoscute morphology (Estes 1983a). These similarities are so strong that Estes (1983a) predicted that "it is possible that the Paramacellodidae will prove a synonym of the Cordylidae" (Estes 1983a: 115).

The family Cordylidae is currently defined as the group including Cordylinae and Gerrhosaurinae (see Estes et al. 1988), which were previously treated as separate families (e.g., Romer 1956). The subfamily Cordylinae has no known fossil record, except for the problematic Pseudolacerta from the upper Eocene or lower Oligocene of France (see Estes 1983a for comments, and also see Auge 1987 for new revision of the genus). The fossil record of Gerrhosaurinae is limited to the Miocene of Africa (Estes 1962; Van Couvering 1979). If future study on further discoveries could confirm the affinity of the Frenchman species to Cordylidae, the specimen SMNH P1927.880 would be the first reported fossil record of the subfamily Cordylinae from Upper Cretaceous deposits in North America.

Genus & species new (B)

Plate 11, Figs. 2-3

Specimen: SMNH P1927.886, P2004.90, both fragmentary dentaries having several teeth and broken bases preserved.

Locality and horizon: Gryde locality, in Sec. 19, Tp. 14, R. 18, W. 3, Frenchman Valley, southwest Saskatchewan; Upper Cretaceous Frenchman Formation (Lancian in age).

Description: SMNH P1927.886 is a fragmentary left dentary, which is short, straight, and deep, but quite robustly built in relation to its small size. The subdental shelf is mediolaterally narrow but dorsoventrally deep below the first eight tooth positions. This part of the subdental shelf is so deep that the ventral edge of the shelf is brought close to the ventral border of the jaw, depressing the anterior part of the Meckelian canal to form an extremely shallow and narrow ventral groove. The shelf posterior to this part is abruptly reduced in depth above what must have been an extensive splenial. The subdental shelf has a dorsal ridge that forms the medial border of the narrow but deep sulcus dentalis. The dentary is anteriorly pointed, indicating a weak mandibular symphysis.

SMNH P1927.886 shows four teeth and the broken bases of six others, representing the first ten tooth positions of the complete tooth row. The teeth are high-crowned, spaced closely together along the tooth row, and are pleurodont, with the lower half of the tooth height attaching to the lateral parapet. The tooth shafts are slender and cylindrical, neither compressed nor expanded. The tooth bases are clearly exposed and lack the heavy deposit of cementum seen in teiids. The bases also show no resorption pits or basal excavation. The crowns can be described as "incipiently tricuspid," as the crown of the ninth tooth has a prominent central cusp and faintly developed side cusps. The posterior cusp is slightly stronger than the anterior one.

The lateral surface of the dentary shows five mental foramina. These foramina are about equal in size and in spacing from one another. Like SMNH P1927.880 (unnamed taxon A, see description above), this dentary also shows tooth marks on both the medial and lateral sides of the jaw.

Discussion: The unnamed taxon B differs from taxon A above primarily in having high-crowned, closely compact, and incipiently tricuspid teeth, and in its substantially smaller size. These differences may be counted as character states that separate the two lizards at the generic level. However, similarities in general jaw shape, in robustness of the subdental shelf, and the nature of the sulcus dentalis suggest that the two taxa should be placed in the same family, either Cordylidae or Paramacellodidae.

As on SMNH P1927.880 (unnamed taxon A), SMNH P1927.886 also shows a paleoecologically significant feature of tooth marks, probably indicative of predation or post-mortem scavenging in a subaerial environment. In addition, the breakage of the first six teeth on the jaw seems to have happened before fossilization, also implying interaction with a predator or scavenger.

Genus & species undetermined

Plate 11, Figs. 4-5

Referred specimens: UALVP 29830, incomplete right maxillary having ten teeth preserved; RTMP 85.36.275, fragmentary left dentary having four teeth preserved.

Locality and horizon: UALVP 29830 was collected in 1969 from MR-4 locality, Verdigris Coulee, near the village of Milk River, southern Alberta; upper member of the Milk River Formation (Aquilan in age). RTMP 85.36.275 was collected from the BB 78 microfossil site (DPP, see Eberth 1990b); Upper Cretaceous Oldman Formation (Judithian in age).

Description: UALVP 29830 consists of an incomplete right maxillary having ten teeth preserved. Although the dorsal process of the maxillary is broken, it shows a sharply descending posterior border, indicating a much shallower posterior part of the bone. Medially above the tooth row is the supradental shelf, which is obviously wider posterior than anteriorly, indicating a prominent palatine process. A large posterior interior alveolar foramen opens close to the midpoint of the tooth row.

The maxillary teeth are pleurodont, with the upper half part of the teeth attached to the lateral parapet of the maxillary. The tooth shafts are strongly compressed anteroposteriorly, giving them a triangular shape in anterior or posterior view. Although strongly compressed, the tooth shafts lack a shoulder-like medial expansion. There are no basal foramina at the tooth bases; instead, several teeth have developed a basal excavation for tooth replacement. The tooth crowns are partially dissolved on this specimen, but enough remains to show that the crowns were more or less chisel-shaped originally, with faint lateral crests. The anterior maxillary teeth are slightly shorter and more slender than the posterior ones.

RTMP 85.36.275 is a left dentary fragment having four teeth preserved. The teeth are closely similar to those on UALVP 29830: they are slightly compressed laterally, more or less chisel-shaped, and have faint anterior and posterior ridges running vertically on the medial side of the crowns. Differences in crown height and other characters suggest that the two specimens may not belong to the same species; however, this possibility cannot be verified at this stage, owing to the fragmentary nature of the specimens. There are no striations on the crown surface. RTMP 85.36.275 represents the very posteriormost part of the dentary, as indicated by its greatly diminished posterior end of the subdental shelf.

Discussion: The two specimens described above were collected from two localities at different geological horizons. They are lumped together as "genus & species undetermined" on the basis of their general resemblances: anteroposteriorly compressed tooth shafts, and more or less chisel-like crowns without striations. These features are Contogenys-like, but poor preservation of the two specimens does not allow a reliable taxonomic referral, even at a familial level. However, the two specimens may not pertain to the same taxon, as RTMP 85.36.275 has taller, and more strongly compressed teeth than does UALVP 29830. They also differ from each other in tooth attachment: RTMP 85.36.275 has half, while UALVP 29830 has one-third, of their tooth height projecting over the parapet of the jaw. Nevertheless, the two poorly preserved specimens are inadequate for me to clearly distinguish them from one another, and to make a reasonable taxonomic assignment. Here, I tentatively place them together as "genus & species undetermined," pending further study on more and better preserved specimens to clarify their taxonomic position.

Infraorder Anguimorpha Furbringer 1900

Family Xenosauridae Cope 1886

The family Xenosauridae as currently defined includes the living Central American Xenosaurus and Asian Shinisaurus (McDowell & Bogert 1954; Estes et al. 1988). Both the skull osteology and the natural history of the two genera are still poorly known; and the monophyly of the family, although supported by 12 synapomorphies (Estes et al. 1988), is still shadowed by the wide geographic separation and distinctively different adaptations of the two genera (see Gauthier 1982; Pregill et al. 1986). The diagnostic characters for this family have been discussed by Estes (1983a) and Borsuk-Bialynicka (1986).

The fossil record of Xenosauridae is poor compared with that of other anguimorphan families. With the exclusion of Nordenosaurus Holman 1973 from Squamata (Gauthier 1982; Estes 1983a), there are only three species in two genera of fossil xenosaurids known from North America (Estes 1983a). In addition, undescribed materials were recently reported from New Jersey (Denton et al. 1991). Several fossil taxa from the Central Asian Gobi Desert also show xenosaurid affinities (Borsuk-Bialynicka 1985), but further study of the Gobi materials is needed to clarify their relationships. In this study, newly discovered specimens from the Lance and Hell Creek formations provide important materials for a better understanding of Exostinus; several specimens from the Milk River Formation represent by far the earliest fossil record of this family, and may provide materials for the recognition of a new xenosaurid taxon in the future.

Exostinus lancensis Gilmore 1928

Plate 12, Figs. 1-6; Text-fig. 20

1928 Exostinus? lancensis Gilmore, p. 23, pl. 26, fig. 2

1928 Harpagosaurus parvus Gilmore, p. 156, fig. 98

1928 Prionosaurus regularis Gilmore, p. 159, Pl. 26, fig. 1

Included specimens: UALVP 29849-29850, incomplete maxillaries; UALVP 29838, dentary; UALVP 29919, frontal; UALVP 29847, 29848, both parietals; UALVP 29920, jugal.

Although collected from outside the study area, these specimens are included in this paper because they represent an important but poorly known North American xenosaurid, which is closely related to the Oldman and Milk River forms of the same group from the study area (see later description).

Locality and horizon: The above-numbered specimens were collected by the UALVP field party from the UCMP V-5616 (AB) and V-5711 (BTB) localities, Lance Formation in eastern Wyoming; and from the BCA locality, Hell Creek Formation, eastern Montana. These specimens are described below.

Known distribution: Upper Cretaceous Lance Formation, eastern Wyoming; Hell Creek Formation, eastern Montana (all Lancian in age).

Diagnosis (revised from Estes 1983a): A Late Cretaceous xenosaurid from North America, differing from the Oligocene Exostinus serratus by the following combination of character states: prefrontal incision of frontal not extend to midpoint of orbit; subdental shelf well-defined, sulcus dentalis present; intramandibular septum more rudimentary; posterior interior alveolar foramen more anteriorly located.

Description: Gilmore (1928) described the holotype maxillary (USNM 10689), and Estes (1964) briefly described the dentary specimens of Exostinus lancensis. Newly discovered specimens from the Lance and Hell Creek formations include a frontal, a jugal, and the anterior end of a maxillary, parts that were unknown for this species before. These specimens provide important information for a better understanding of this fossil xenosaurid, and hence are described below.

Maxillary.-Two incomplete maxillaries (UALVP 29849, 29850), both from the BTB locality of the Lance Formation, are referrable to Exostinus lancensis on their tooth form and the sculpture on the lateral surface. UALVP 29849 is the anterior part of a right maxillary, having the six anteriormost tooth positions preserved. The lateral surface of the maxillary is extensively ornamented with flattened patches of "vermiculate sculpture" (Gauthier 1982; Estes et al. 1988) that are separated by shallow grooves (Plate 12, Fig. 1). At the lower border of the ornamentation, the superior alveolar foramina are small and circular, as in the holotype (USNM 10689, see Estes 1964). The maxillary has a prominent premaxillary process, behind which the vertical nasal process is slightly notched for the posterior border of the external narial opening; it then gently turns dorsoposteriorly. In medial view, the anterior palatal process (or the vomerine process) of the maxillary is stronger than the lateral premaxillary process, and is plate-like, with its widened base as the anterior extension of the supradental shelf. This medial process diverges from the lateral process at about a 45 degree angle. The supradental shelf is clearly defined, and a slight supradental gutter can be seen.

The six tooth positions preserved consist of five teeth and the space for another. Most of the teeth are broken, but the third is complete, clearly showing that the tooth crown is unicuspid, slightly recurved, and having a longer and slightly trenchant anterior cutting edge; no striations are present. The tooth shafts are subcylindrical and thick-walled, and the tooth bases are firmly cemented to the lateral parapet. These teeth are pleurodont, having about two-thirds of their height attached to the lateral parapet. Of the five teeth preserved, three clearly show a resorption cavity. The third tooth has almost half of its base resorbed, indicating a direct replacement mode (in agreement with Estes 1964; but in conflict with McDowell & Bogert 1954, who stated that the xenosaurs have interdental replacement).

Another specimen, UALVP 29850, is the posterior end of a left maxillary, which is broken at the posterior interior alveolar foramen in front of the fifth tooth position from the back. Although fragmentary, this specimen shows the same tooth form and osteodermal ornamentation as the holotype maxillary described and figured in Gilmore (1928). It is worthwhile to note here that this fragment preserves a structure unknown from other specimens: the last two maxillary teeth are sharply reduced in size corresponding to a sigmoid twist at the posterior part of the supradental shelf, at the maxillary-jugal articulation.

Frontal.-UALVP 29919, a fragmentary frontal (Plate 12, Fig. 3) from the BCA locality, is clearly referrable to Exostinus lancensis, as it is characteristically of xenosaurid type (fused along the mid-line and hourglass-shaped) and is heavily ornamented with osteoderms like those on the holotype maxillary. This frontal differs from that of Restes rugosus (Gilmore 1942a) Gauthier 1982 in having a prominent crust of tuberculate osteoderms (rather than flattened tesserae), and differs from that of Exostinus serratus (type species) in having larger and fewer tuberculate osteoderms, with a less complex surface texture. The ventral view of the specimen shows that frontal fusion is complete, with the midline suture barely recognizable. The right subolfactory process is entirely broken off, but the left side shows that the two processes held a trough-like subolfactory track, and tend to meet at the ventral midline. In lateral view, the left anterior corner of the bone shows a clearly defined prefrontal incision, the posterior extension of which does not reach the midpoint of the orbit.

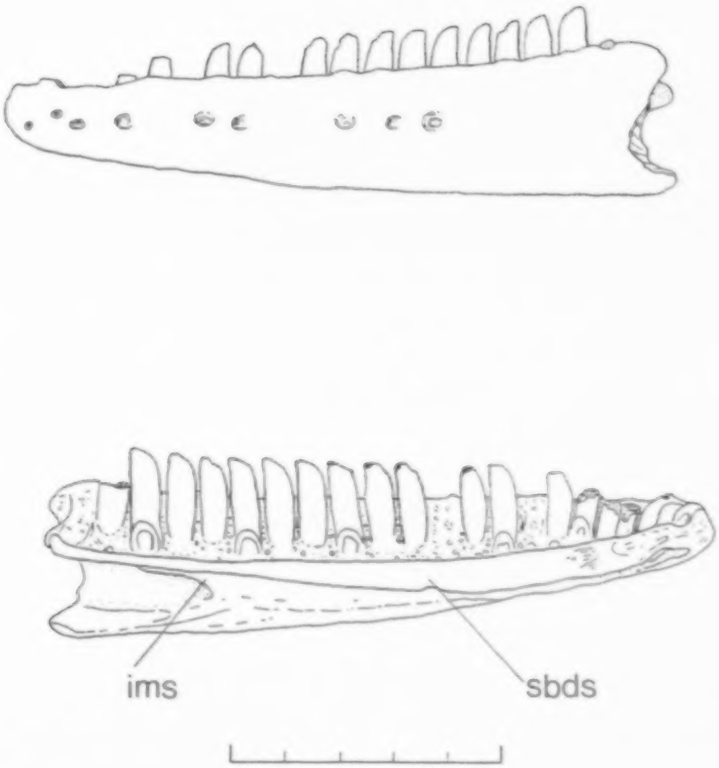
Parietal.-Two parietals (UALVP 29847 from the BTB locality and UALVP 29848 from AB locality) are referred to Exostinus lancensis, as they display osteoderms, with a "vermiculate sculpture," which is considered to be synapomorphic for the Xenosauridae (Estes et al. 1988). UALVP 29847 shows a widened lateral border, implying suppression of the supratemporal opening and a short supratemporal process. UALVP 29848 shows that the parietal is a fused, single unit. Both specimens show that the oesteodermal ornamentation is heavy anteriorly but diminished posteriorly.

Jugal.-UALVP 29920 from the BTB locality, Lance Formation is the only jugal known that can be referred to Exostinus lancensis. The large size of this jugal indicates an individual larger than the other elements referred to this species, but it is of a characteristically xenosaurid type, with the postorbital branch widened and sculptured (Gauthier 1982; Estes et al. 1988). The sculpture pattern is similar to that on the frontal and parietals; therefore, these disarticulated specimens can be referred to the same species, in spite of their size differences. The jugal is large, wide, and is heavily ornamented with tuberculate osteodermal mounds on the lateral surface. Similar, but much smaller, osteodermal mounds coalesce along the posterior and ventral border of the orbit. The anteroventral process (maxillary process) is elongated and thickened, forming most of the ventral border of the orbit. Although incomplete, the anterior end of this process bears a ventral crest, which fits in the posterior groove of the maxillary above the supradental shelf. The dorsal process (postorbital process) of the jugal is largely broken off, but the base shows it was widened and extensively ornamented (a synapomorphy of the Xenosauridae; Gauthier 1982).

Dentary.-The dentary structure of Exostinus lancensis is not well known, except for Estes' (1964) brief description. UALVP 29838 from the BTB locality represents by far the most complete dentary for this species, and provides the material for more extensive description of the dentary than was possible before. The dentary is elongate, lightly built, and relatively straight in dorsal view (Estes 1964). Medially, it bears a horizontally straight, slender, but clearly defined, subdental shelf, which has a dorsal ridge bordering a shallow sulcus dentalis. The shelf gradually increases its depth anteriorly until the eighth tooth position, where it reaches its maximum depth (about one-third of tooth height) and starts curving medially towards the mandibular symphysis. The Meckelian canal is anteriorly narrow and open ventrally below the first eight tooth positions; it increases in depth and width posteriorly, indicating that a relatively large splenial covered the most ventromedial aspect of the dentary (Estes 1964). The maximum depth of the Meckelian canal is about equal to the tooth height. Both dorsal and ventral splenodentary articulating surfaces terminate anteriorly under the ninth tooth position. The large posterior interior alveolar foramen opens into Meckelian canal under the 18th and 19th teeth. As Gauthier (1982) has noted, this location is more anterior than that in the Oligocene Exostinus serratus. The intramandibular septum of the Meckelian canal (sensu Estes et al. 1988) retains a primitive configuration: the septum is obliquely directed and lacks a free ventral border. This condition is similar to that in Recent Xenosaurus grandis (see Gauthier 1982, fig. 44) and some skinks (e.g., Mabuya macularia, pers. observ.), but is different from the advanced anguid condition, in which the septum is vertically directed and develops a free ventral border (Estes 1964).

The dentary containing a nearly complete tooth row, consisting of 22 tooth positions (12 well-preserved teeth and tooth bases as well as spaces for ten others). I estimate that only the last one or two teeth are missing. The dentary teeth are closely spaced, and are pleurodont, with slightly less than one-third of the tooth height projecting above the lateral parapet. The tooth shafts are subcylindrical, lacking either compression or expansion. The tooth crowns are slightly compressed laterally and recurved, having the leading cutting edge much longer than the posterior one, giving the teeth a dagger-shaped appearance. The tooth crowns are not serrated along the cutting edge, nor are they striated on the medial and lateral surfaces (contrary to Estes 1964, who described the teeth as having "faint lingual striations"). Although several teeth have their anterior cutting edge chipped, as if they were "bicuspid", well-preserved teeth clearly show no indication of a second cusp or cuspule on the crowns. This observation is contrary to Estes (1964) and Gauthier (1982), who described the teeth as "slightly bicuspid" or "incipiently bicuspid" (Estes [1965: 104] suggested that "the condition is better described as bilobate, as in many Anguidae"). The five anteriormost teeth are not preserved, but the remainder show that the dentary teeth of this lizard are homodont (isodont), without differentiation of tooth form along the tooth row, except that the anterior ones are slightly more slender than those more posterior. Several teeth on the specimen clearly show that deep replacement pits are developed lingually in the tooth bases, implying a direct tooth replacement mode (Edmund 1969).

The lateral surface of the dentary is smooth and is only weakly convex at the posterior part of the bone. Nine unequally spaced inferior alveolar foramina open laterally, with the posteriormost one located lateral to the 15th tooth position.



Text-fig. 20. Xenosauridae, Exostinus lancensis, Lance Formation, eastern Wyoming; UALVP 29838, nearly complete right dentary; (above) lateral view, (below) medial view. Scale = 5 mm. Abbreviations as in Text-fig. 2.

Discussion: The family Xenosauridae is a problematic taxon, which includes two geographically and ecologically widely separated living forms, *Xenosaurus* and *Shinisaurus*. The monophyly of the family is still questionable and the evolutionary history of the family is poorly understood because of its scanty fossil record. The North American fossil record of the family includes only three species in two genera: the Oligocene *Exostinus serratus* Cope 1873, the late Paleocene and early Eocene *Restes rugosus*, and the Late Cretaceous *Exostinus lancensis*. These fossil taxa are mostly based on disarticulated materials that are anatomically not comparable between the species. Gauthier (1982) separated *Restes rogosus* from *Exostinus* on "its unique cephalic osteoderms" and pointed out that *Exostinus lancensis* could well be generically distinguishable from the type species *Exostinus serratus*. On the basis of new evidence revealed from the newly discovered specimens, I offer the following comments on this important but problematic taxon.

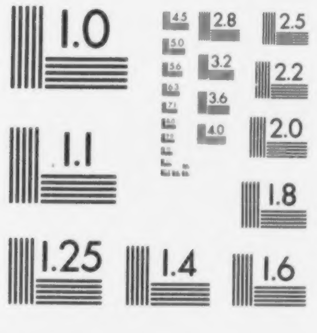
The fossil genus *Exostinus* Cope 1873 (also see Cope 1884, 1886) consists of two species: *Exostinus serratus* (type species, see Cope 1873) and *E. lancensis* Gilmore 1928. These two taxnomic names are "nomina inquirenda" (sensu Mones 1989: 233), since they "are based on remains not comparable with other closely related taxa and those identity is presently not demonstrable" (ibid.). Gauthier (1982) suggested that *E. lancensis* should be removed from *Exostinus*, while Estes (1983a) explained the difficulty in taking such a course, owing to the lack of materials that are anatomically directly comparable between the two species; the type series of *E. serratus* consists of a frontal, a jugal, and a dentary, while these elements are unknown for *E. lancensis* (the holotype of the latter species is a maxillary). Now, with the discovery of the frontal (UALVP 29919) and the jugal (UALVP 29920) that are of "*Exostinus lancensis*-type," Gauthier's suggestion seems to be more plausible. The newly recovered frontal specimen shows that the prefrontal incision does not extend to the midpoint of the orbit, and hence, is significantly different from that of the Oligocene *Exostinus serratus* or that of the Paleocene-Eocene *Restes rugosus*. The jugal and dentary specimens of the Lancian "*Exostinus lancensis*" are also significantly different from the same elements of *Exostinus serratus*, as mentioned in the description above. These differences are apparently great enough to separate the Lancian *Exostinus lancensis* from the Oligocene *Exostinus serratus* at a generic level; therefore, a new generic name should be proposed for the Lancian species. However, it is premature to make such a revision in this paper, before the type specimens of the type species *Exostinus serratus* are carefully examined. Therefore, *Exostinus lancensis* is retained in this paper as a valid name.

Estes et al. (1969) referred an unfused frontal (MCZ 3662b) from the Hell Creek Formation to *Exostinus lancensis*. The specimen was not figured, but the description of it raises some uncertainty about this identification: First, Estes et al. (1969: 20) claimed that "the frontal (MCZ 3662b) may be referable to *E. lancensis* on the basis of dermal sculpture pattern;" then they stated that "it [the frontal] is eroded, and because of this and its small size, it does not display a sculpture pattern as well-developed as that on the larger Lance Formation parietal referred by Estes (1964, pl. 3)." With the discovery of new frontal material from the same horizon of definitely *Exostinus lancensis* type, the identification of MCZ 3662b is uncertain. In Recent xenosaurids, frontals are fused in the embryo (Estes et al. 1988). This, together with new fossil evidence, indicates that fused frontal is a primitive character within the Xenosauridae.

Estes (1964) misspelled *Harpagosaurus* Gilmore 1928 as "*Marpagosaurus*" in the caption for his plate 5, and later (1983a: 130) listed "*Marpagosaurus parvus*" as a synonym of Gilmore's *Harpagosaurus parvus* (= *Exostinus lancensis* Gilmore 1928). In this particular case, Estes' "*Marpagosaurus*" is an "incorrect subsequent spelling" (not an available name), that has no standing in zoological nomenclature, and hence, should not be recorded in synonymy (ICZN 1985, article 33c).

3

PM-1 3½"x4" PHOTOGRAPHIC MICROCOPY TARGET
NBS 1010a ANSI/ISO #2 EQUIVALENT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PRECISION^SM RESOLUTION TARGETS

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?Exostinus sp.

Plate 12, Fig. 7

Referred specimen: UALVP 944, a small but completely co-ossified frontal.

Locality and horizon: Outcrop of the Upper Cretaceous Oldman Formation, in S. 29, Tp. 21, R. 12, W. 4 (the old "Steveville" locality); southern Alberta, Canada.

Description: UALVP 944 is the posterior part of a fused frontal, and is the only specimen of this type known from the Oldman Formation. Although small, the frontal is so well co-ossified as a single unit that the ventral surface shows no midline suture. The subolfactory processes are broken on both left and right sides, but the broken bases suggest that the processes were ventrally directed and probably not in contact at the midline.

In dorsal view, the specimen shows important characters on which its taxonomic assignment is based: it is strongly constricted between the orbits, giving an hourglass shape to the bone; and small tuberculate osteoscutes having a vermiculate sculpture are fused to its external surface. These osteodermal mounds are all about equal in size and are separated from each other by deep and wide grooves. The specimen is too incomplete to show the prefrontal or postfrontal incision.

Discussion: UALVP 944 is the first xenosaurid specimen known from the Oldman Formation, which is about 11 Myr older than the Lance and Hell Creek formations (Thomas et al. 1990), from which Exostinus lancensis is known. The wide geologic gap, and more importantly the different osteodermal sculpture, clearly distinguish the Judithian morph from the Lancian E. lancensis.

It is worth while pointing out that the osteodermal sculpture of the Judithian form is structurally more closely similar to those of the Oligocene *Exostinus* *serratus* (see Gauthier 1982, fig. 7) than to either Lancian *E*. *lancensis* or the Paleocene *Restes* *rugosus* (see Gauthier 1982, fig. 5). This condition may suggest that two different lineages are involved in the evolutionay history of the Xanosauridae. However, the fossil record for these taxa is so poor that many taxonomically important characters are unknown as yet. Clarification of their phylogenetic relationships must wait discovery of more nearly complete material.

Sahni (1972) reported two xenosaurids from the Judith River Formation by referring two maxillaries (AMNH 8497, 8498) to "*Exostinus* *lancensis*" and "cf. *Exostinus* sp.." AMNH 8498 (Sahni 1972, fig. 8E-F), a left maxillary, has cylindrical tooth shafts without basal infoldings (tooth crowns broken off), and is similar in that aspect to *Exostinus*. But the sculpture pattern on the lateral surface is not comparable to that in the type species *E*. *serratus* (in which maxillary is poorly known), and is clearly different from that of *E*. *lancensis* (compare Sahni 1972, fig. 8E-F with Estes 1964, pl. 5). Therefore, it is possible when more nearly complete specimens are found that the Judithian form will prove to be generically different from *Exostinus*. Another specimen, AMNH 8487, is too fragmentary to provide a valid basis for its referral to *Exostinus* *lancensis*, and seems to be indistinguishable in tooth form from AMNH 8491 (Sahni 1972, fig. 8K), a maxillary that Sahni referred to *Leptochamops* *denticulatus* (see relevant discussion above).

Xenosauridae, Genus & species undetermined

Plate 12, Figs. 8-10

Specimens: UALVP 29914, jugal; UALVP 29915-29918, incomplete maxillaries (also four unnumbered speciemens).

Locality and horizon: MR-6 locality, Verdigris Coulee, approximately 30 km east of the village of Milk River, southern Alberta; upper member of the Milk River Formation (Aquilan in age).

Description: UALVP 29914 (Plate 12, Fig. 8) is an incomplete right jugal with both of its posterodorsal and anteroventral processes broken. The jugal is substantially smaller than that of Exostinus lancensis (see UALVP 29920 described above), but is proportionally compatible to the maxillaries described below from the same locality and horizon. Unlike the Lancian Exostinus lancensis and Recent xenosaurs, the posterodorsal process of this jugal is narrow, probably the primitive condition. However, the lateral surface is of xenosaurid-type, with vermiculate rugosities on the postorbital branch of the bone. These rugosities are less prominent and arranged in a more random pattern than those in Exostinus lancensis, which are concentrated to form tuberculate mounds.

Four maxillaries (UALVP 29915-29918) are tentatively identified as "Xenosauridae, genus & species undetermined" from their fused osteodermal ornamentation on the lateral surface. UALVP 29915 (Plate 12, Fig. 9) is the anterior part of a left maxillary, with three broken teeth and vacant spaces for two others. Part of the dorsal process is preserved; the lateral surface is extensively ornamented with vermiculate sculpture. The sculpture is as extensive as, and is similar in pattern to that of Exostinus lancensis (compare with UALVP 29849, Plate 12, Fig. 1), but the tubercles are less prominent and less concentrated than in that species. Another specimen (UALVP 29918), the anterior part of a right maxillary, shows the same sculpture pattern. As in the Lancian Exostinus lancensis, the superior alveolar foramina are small, circular, and are equally spaced.

UALVP 29916-29917 are the posterior part of maxillaries, both showing a small palatine process associated with a small posterior interior alveolar foramen. The tooth form of this Milk River xenosaurid is best shown in UALVP 29917, which has two complete teeth preserved. The two teeth are posterior to the posterior interior alveolar foramen and probably represent the sixth and fifth positions from the back. The teeth are pleurodont and slightly recurved. The crowns are trenchant, with sharp anterior and posterior blades, but are not serrated. As in other anguimorphans, the tooth bases bear a small medial foramen. The bases are not expanded and also have no basal infoldings, differing in these respects from those in the Varanoidea.

Discussion: The specimens described above from the upper member of the Milk River Formation represent the earliest fossil record for the family Xenosauridae, as the age of the formation has been determined as Aquilan or early Campanian (L. S. Russell 1964; Williams & Burke 1964; Fox 1976; Lillegraven & McKenna 1986; Lillegraven 1991). The taxonomic assignment of this early xenosaurid is difficult, because all the specimens known are fragmentary and other fossil taxa of the same group are still poorly understood (see above discussion). Morphologically, the Milk River jugal (UALVP 29914) is clearly distinguishable from those of the Lancian Exostinus lancensis and Oligocene E. serratus by its narrow, less heavily sculptured postorbital branch. The sculpture pattern on the lateral surface of the maxillaries (UALVP 29915-29918) closely resembles that on the maxillary that Sahni (1972) described from the Judith River Formation, eastern Montana, but is different from that in the Lancian Exostinus lancensis. The resemblance may suggest that the Milk River and Judith River materials are congeneric; however, a reliable taxonomic assignment of these fossils must wait the discovery of better preserved specimens.

Finally, it must pointed out that there is no direct evidence for the association of the Milk River jugal with the maxillaries discussed above. These materials are tentatively placed together, leaving only one xenosaurid lizard recognized from the Milk River Formation. However, further study on more extensive materials could well change this association.

Family Anguidae Gray 1825

Genus *Odaxosaurus* Gilmore 1928

Type species: *Peltosaurus*? *piger* Gilmore 1928.

Range: Upper Cretaceous, North America. Several Paleocene and Oligocene specimens were previously referred to *Odaxosaurus* (Meszoely 1970; Estes 1975, 1976; Sullivan 1979a,1981, 1982), but have been lately placed in *Proxestops* Gauthier 1982 or *Machaerosaurus* Gilmore 1928 (see Gauthier 1982; Estes 1983a; Sullivan 1986b). Accordingly, the geologic range of *Odaxosaurus* may not extend to the Paleocene; for pre-Lancian *Odaxosaurus*, see later discussion.

Diagnosis: As for the type species, and see discussion below.

Odaxosaurus *piger* (Gilmore 1928)

Plate 13; Figs. 1-4

1928 *Peltosaurus*? *piger* Gilmore, p. 136, pl. 26, figs. 4, 6

1928 *Odaxosaurus* *obliquus* Gilmore, p. 158, pl. 26, figs. 3, 5

1964 *Peltosaurus* *piger* -- Estes, p. 119

1970 *Pancelosaurus* *piger* Meszoely, p. 105

Holotype: USNM 10687, incomplete right dentary with six posterior teeth. Collected by O. A. Peterson in 1889, from "Peterson's quarry," Lance Creek, Niobrara County, eastern Wyoming (Gilmore 1928).

Referred specimens: Scollard Formation, KUA-3 locality: dentary - UALVP 33381; Frenchman Formation, Wounded Knee locality: maxillary - UALVP 33382.

Known distribution: Upper Cretaceous Lance Formation, eastern Wyoming; Hell Creek Formation, eastern Montana; Laramie Formation, Colorado (Carpenter 1979); Scollard Formation, central Alberta; and Frenchman Formation, Saskatchewan (all Lancian in age). Some specimens of Judithian and Paleocene age have been referred to this species, but none of the referrals are convincing (see later discussion).

Diagnosis (from Estes 1983a: 147): "Differs from other glyptosaurine lizards in having paired frontals (which may fuse in Paleocene individuals if correctly referred); vermiculate (non-tubercular) osteoscute sculpture; rectangular osteoscutes with poorly-developed lateral bevels; teeth obtuse, shafts expanded transversely, crowns squared-off with an anteroposteriorly-oriented but slightly oblique cutting edge striated lingually and labially" (see discussion below).

Description: UALVP 33381 from the KUA-3 locality (Scollard Formation) consists of an incomplete left dentary with seven tooth positions preserved (three teeth and broken bases as well as vacant spaces for four others). This specimen is referred to Odaxosaurus piger as it shows the same tooth form and dentary structure as the type Lance specimens (see Gilmore 1928; Estes 1964). As in the Lance specimens, this dentary bears pleurodont teeth, which have subrectangular bases, anteroposteriorly compressed and medially expanded shafts, and chisel-shaped crowns with a horizontal cutting edge and vertical striations. These are the diagnostic characters recognized by Gilmore (1928) and Estes (1964) for Odaxosaurus piger. The dentary is posteriorly broken at the anterior inferior alveolar foramen, and hence, the notch for the foramen on the tooth-bearing border is not preserved, nor is the intramandibular septum posteriorly within the Meckelian canal.

UALVP 33382 from the Wounded Knee locality (Frenchman Formation) is a left maxillary with nine tooth positions (seven teeth and broken bases for two others). The referral of this maxillary to Odaxosaurus piger is principally on a large posterior interior alveolar foramen that is associated with a large palatine process. These characters are distinct for Odaxosaurus, and are different from gerrhonotines, which have a much smaller or no palatine process and have two posterior interior alveolar foramina (Meszoely 1970; and pers. observ.). As a result of erosion, the tooth crowns show no horizontal cutting edge, and vertical striations, but enough remains to show that the teeth are squared-off and laterally compressed. The tooth bases are like those of specimens from the Lance, subrectangular in shape and bearing a small basal foramen.

In addition to the specimens described above, thirteen maxillaries and 27 dentaries from the Lance and Hell Creek formations are included in this study because these specimens provide new information for a better understanding of Odaxosaurus piger, and provide comparative materials for the study of the Scollard and Frenchman specimens. The Lance specimens were collected from the BTB locality, and include one maxillary (UALVP 29851) and five dentaries (UALVP 29852-29856). The Hell Creek specimens were from the BCA locality, and include 12 maxillaries (UALVP 29857-29861, 29879-29885) and 22 well-preserved dentaries (UALVP 29862-29878, 29886-29890).

UALVP 29851 (Plate 13, Fig. 2) is an incomplete right maxillary having four teeth preserved. Although incomplete, the specimen is of importance as it shows unworn tooth crowns and the osteoscute sculpture on its lateral surface. The marginal teeth of this lizard have the characteristic combination of a chisel-shaped lateral cutting edge (previously known) and a remnant medial cusp (unknown before). A well-preserved dentary (UALVP 29852) shows the same crown pattern, while most of the other specimens have no medial cusp as the result of wear. The tooth crowns are striated both lingual and labially, but the lingual striations are obviously stronger than those on the labial side. An osteoscute is fused to the lateral surface of the maxillary (a similar structure is seen on UALVP 29887, a dentary from the BCA locality). The osteoscute is thick and tuberculate, rather than flattened plate, and different from those on the previously referred parietals and frontals (see Estes 1964, 1983a), which basically have a gerrhonotine-diploglossine type of sculpture (Estes 1964; Meszoely 1970).

The crown pattern of the dentary teeth is best shown on UALVP 29852, an incomplete left dentary having nine teeth and the spaces for four others. As in the maxillary described above, the teeth of this specimen show a combination of a chisel-like lateral cutting edge with a remnant medial cusp. However, this crown pattern varies along the tooth row: the slightly procumbent anterior teeth have a less well-developed cutting edge but a stronger medial cusp, while the posterior teeth, which are shorter than the anterior ones, have a stronger cutting edge and a weaker medial cusp. The Meckelian canal is anteriorly restricted to form a shallow and ventrally-facing groove, but gradually turns more ventromedially in the posterior half of the dentary. The ventral edge of the tooth-bearing border bears a lateral extension in front of the anterior inferior alveolar foramen, forming a flat surface for attachment of the splenial.

Discussion: The lizard Odaxosaurus piger has a complex taxonomic history, one in which its taxonomic name has been changed several times. Gilmore (1928) named and described Peltosaurus? piger (Gilmore 1928: 136) and Odaxosaurus obliquus (Gilmore 1928: 158), based on several specimens from the Lance Formation, eastern Wyoming. Estes (1964) synonymized Odaxosaurus obliquus with Peltosaurus? piger, and firmly referred the species to Peltosaurus Cope 1872; meanwhile, he also provided solid evidence for the familial assignment of Peltosaurus piger to Anguidae from the construction of the dentary. More recently, Meszoely (1970) removed the species from Peltosaurus on differences in jaw and osteoscute sculpture, and named a new genus, Pancelosaurus, for Peltosaurus piger. Meszoely et al.

(1978) published the most recent revision of the genus, and finally clarified the taxonomic status of this species. They reviewed all of the nomenclatural controversy, restudied the holotype of *Odaxosaurus obliquus*, and came to the following conclusions:

1) Gilmore's *Odaxosaurus obliquus* is indistinguishable from *Peltosaurus*? *piger*.

2) Gilmore's *Peltosaurus*? *piger* is generically different from *Peltosaurus*, and should be removed from the genus.

3) *Pancelosaurus* Meszoely (1970) is a synonym of *Odaxosaurus* Gilmore (1928).

4) According to ICZN rules, both the generic name "*Odaxosaurus*" and specific epithet "*piger*" have priority; thus, the proper name for this lizard is *Odaxosaurus piger*.

Gilmore (1928) classified *Odaxosaurus piger* (his "*Peltosaurus*? *piger*") in the Anguidae, and first noticed its similarity in tooth form to *Glyptosaurus* Marsh 1871. This familial palcement was questioned by McDowell and Bogert (1954), but has been solidly confirmed by Estes (1964) on the basis of dentary structures. However, the taxonomic status of *Odaxosaurus piger* at the subfamilial level is still in dispute. The family Anguidae is commonly subdivided into four subfamilies: Anguinae, Glyptosaurinae, Gerrhonotinae, and Diploglossinae (see, e.g., McDowell & Bogert 1954; Meszoely 1970; and also see Estes 1983a for a different classification). Meszoely (1970) recognized the basal position of *Odaxosaurus* in anguid phylogeny, and referred it to the subfamily Anguinae on the basis of its *Ophisaurus*-like osteoscutes. Sullivan (1982) proposed a subfamilial name Odaxosaurinae for *Odaxosaurus piger*, separating this species from Glyptosaurinae on the basis of its non-tubercular osteoscutes. This idea is further developed in his later publications (see Sullivan 1986a-b). After carefully evaluating the character states of this lizard, Estes (1983a) put greater weight on tooth morphology than sculpture pattern of the osteoscutes, and classified *O. piger* in the Glyptosaurinae, as its most primitive member (Estes 1983a: 148).

The evidence that Sullivan used to separate *Odaxosaurus* from the Glyptosaurinae as a subfamily is quite problematic: first, the holotype of *Odaxosaurus piger* is a dentary with teeth, not a skull element with osteoscutes; thus, characters of tooth morphology and dentary structures must be relied on for interpreting the relationships of this lizard. Second, the referral of those parietals and frontals having non-tuberculated osteoscutes to Odaxosaurus piger is questionable, as two jaw specimens (UALVP 29851 and UALVP 29887) show osteoscutes different from those on the referred parietals and frontals (thick tuberculate mounds vs. thin plates with a vermiculate sculpture). The referral of the Lance disarticulated parietals and frontals to O. piger is mainly based on size and relative abundance of individuals (see Meszoely 1970: 105). Estes (1964: 122) pointed out that "the pitted and ridged sculpture pattern of these osteoscutes resembles most Recent Gerrhonotus." Meszoely (1970) correctly pointed out that: "The frontals of Odaxosaurus piger resemble closely those of Recent Diploglossus; they agree in general outline .... and in having nearly identical sculpture on the osteoscutes covering these bones" (Meszoely 1970: 108). However, Estes (1983a) noted that the species has a derived, glyptosaurine-like tooth form. Here, we have a Cretaceous anguid lizard with a glyptosaurine type of teeth and jaw structure but diploglossine type of skull elements and osteoscutes, with the skull elements based on size and relative abundance of the fossils. Therefore, the question is whether this referral is correct or the skull elements actually represent an anguid lizard other than Odaxosaurus. In fact, Armstrong-Ziegler (1980: 21) has already questioned this referral by stating that "the dentaries of both Gerrhonotus and Pancelosaurus occur in the Lance Formation; Meszoely (1970, p. 105) assigned the above defined osteoscutes to Pancelosaurus instead of Gerrhonotus on the basis of the greater abundance of skull remains of Pancelosaurus relative to Gerrhonotus. This criterion of relative abundance used by Meszoely does not seem sufficient reason to assign these osteoscutes to Pancelosaurus or Gerrhonotus." The discovery of the jaw materials with osteoscutes (see description above) and the discovery of advanced glyptosaurine-type osteoscutes from Judithian beds in New Jersey (Denton et al. 1991) implies more strongly than before that the association of these disarticulated materials is uncertain.

It is evident that the early history of Anguidae involved two major evolutionary lines: the Diploglossine (Gerrhonotine) line and the Glyptosaurine line. The former includes those anguids that are essentially predatory, with sharp teeth and thin non-tuberculated osteoscutes; and the latter line includes those non-predatory anguids having obtuse teeth with a thick enamel cap for a duraphagous diet, and a heavy armour of thick tuberculated osteoscutes. The recent discovery of glyptosaurine-type body scutes from New Jersey (Denton et al. 1991) indicates that the tuberculated scutes occurred as early as mid-Campanian or even earlier. From jaw structure and tooth morphology, Odaxosaurus piger is obviously on the glyptosaurine line; and the skull elements previously referred to O. piger are possibly associated with some kind of predatory anguid, as the osteoscute sculpture on these bones is closely similar to the Diploglossus-Ophisaurus type (Estes 1964; Meszoely 1970). This type of osteoscute is also known from the Oligocene Parophisaurus Sullivan 1987, the anguid lizard that is ideal for the structural ancestor of Ophisaurus (see Sullivan 1987).

Odaxosaurus piger is only known from the Lancian horizons, including the Lance, Hell Creek, Laramie, Scollard, and the Frenchman formations. Several Paleocene and Oligocene specimens were previously referred to this species (Meszoely 1970; Estes 1975, 1976; Sullivan 1979a, 1981, 1982), but have recently been re-assigned to Proxestops jepseni or Machaerosaurus (see Gauthier 1982; Estes 1983a; Sullivan 1986b); therefore, no definite Odaxosaurus piger is known from post-Lancian horizons. Pre-Lancian Odaxosaurus lizards were previously reported from Judith River Formation (Sahni 1972), Mesaverde Formation (see Estes 1983a), and from the Oldman Formation (Fox 1976). My study of the specimens from the Oldman Formation reveals that the Judithian Odaxosaurus may represent another species different from Lancian O. piger, if the differences between the two are not in fact great enough to separate them at the generic level (see following description and discussion).

Odaxosaurus priscus n. sp.

Plate 13, Figs. 5-10; Text-fig. 21

Holotype: UALVP 29896, an incomplete right dentary with eight teeth and spaces for six others.

Type locality and horizon: Outcrop of the Oldman Formation near Irvine, in S 31, Tp. 11, R 2, W 4, about 40 km east of Medicine Hat, southeastern Alberta; Upper Cretaceous Oldman Formation (Judithian in age).

Referred specimens: Railway Grade locality: UALVP 29892, maxillary. Irvine locality: UALVP 29891, 29893-29895, maxillaries; UALVP 29897-29902, 33380, dentaries.

Known distribution: Type Irvine and Railway Grade localities, Oldman Formation, southeastern Alberta.

Diagnosis: A Judithian Odaxosaurus differing from the Lancian O. piger in the following combination of character states: dentary more robustly built and more laterally convex; dentary teeth fewer, less truncate; intramandibular septum shallow, with free ventral border extending anteriorly to the midpoint of tooth row.

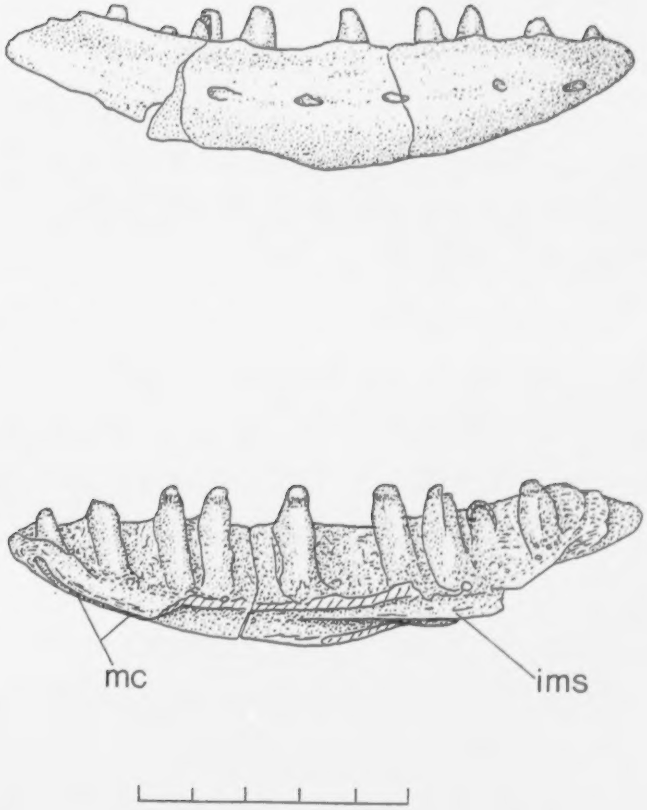
Etymology: priscus (L.), meaning "former, aboriginal."

Description: The holotype (UALVP 29896) is a right dentary showing that the jaw configuration of this lizard is similar to that of the Lancian Odaxosaurus piger; however, the dentary is more heavily built and laterally convex than in the latter species. This specimen retains a complete tooth row, with eight teeth and the spaces for six others, giving a total of 14 positions. As in O. piger, the tooth shafts are strongly compressed anteroposteriorly and have a strong, shoulder-like, medial expansion. The tooth crowns on this specimen are partially dissolved, but are apparently less truncated than those in Odaxosaurus piger, especially for the anterior and middle teeth. These teeth of are also more widely spaced than in Odaxosaurus piger.

Medially, most of the tooth-bearing border (subdental shelf) has been broken away; thus, the notch for the anterior inferior alveolar foramen is not shown on this specimen. However, four other dentaries (UALVP 29897-29898, 29900, 29902) clearly show that the notch forms the dorsal and anterior border of the anterior inferior alveolar foramen. The Meckelian canal is as ventrally restricted as in O. piger, but the intramandibular septum is shallower, and less vertically directed compared to the latter, and has a free ventral border extending anteriorly to the midpoint of the tooth row.

Another dentary, UALVP 29897, has seven teeth and the base for four others preserved. The crowns of most of the teeth are badly worn, but one posterior tooth (probably the fourth from the back) clearly shows that the crown is chisel-shaped. The sulcus dentalis is entirely lacking, and the subdental shelf is greatly reduced to form a smooth sloping border with a small notch for the anterior inferior alveolar foramen. Like the holotype, this dentary also shows that the free ventral border of the intramandibular septum extends anteriorly beyond the anterior inferior alveolar foramen to the midpoint of the tooth row, differing in that respect from Odaxosaurus piger, in which the septum extends only to the point below the foramen (Text-fig. 21).

The dentary teeth are best shown on UALVP 33380, a specimen from the Irvine locality. On this specimen, two well-preserved posterior teeth above the intramandibular septum show that the tooth shafts, like those of Odaxosaurus piger, are anteroposteriorly compressed and have a shoulder-like medial expansion. However, unlike the posterior teeth in O. piger, the two teeth have slightly recurved crowns with faint medial striations (but lack lateral striations). Well-preserved posterior teeth on UALVP 29894, a maxillary, consistantly show the same type of crown pattern (see later description).



Text-fig. 21. Anguidae, Odaxosaurus priscus n. sp., Oldman Formation, southeastern Alberta; UALVP 29896 (holotype), incomplete right dentary; (above) lateral view, (below) medial view. Scale = 5 mm. Abbreviations as in Text-fig. 2.

Among the five maxillaries referred to this species, two are obviously better preserved than the others. UALVP 29892 (Plate 13, Fig. 7) from the Railway Grade locality is from the right side, and bears four teeth, and the bases as well as spaces for seven others. The specimen shows essentially the same configuration as that of Lancian Odaxosaurus piger, but has a much more prominent premaxillary process. The posterior interior alveolar foramen is single, large, and located above the ninth or the tenth tooth position from the front. Unlike the maxillary in the Lancian species, however, this specimen shows that the crowns of the anterior and middle teeth are bluntly unicuspid, slightly recurved, but clearly show a tendency towards development of a lateral cutting edge. In occlusal view, the tooth crowns have a central cusp that curves lingually and posteriorly, forming an "inwardly pointing V" (see Estes 1964). The medial striations on these teeth are much weaker than in O. piger and the lateral surfaces show no striations at all on this specimen. The posterior teeth of UALVP 29892 are not preserved, but must have had chisel-shaped crowns, as clearly shown on the dentary specimens.

Another maxillary, UALVP 29891, is from the left side and has five teeth and the bases for four others. Like UALVP 29892, this specimen also shows a prominent premaxillary process (Plate 13, Fig. 9). The lateral parapet of the maxillary is broken immediately behind the ninth tooth position, but it still clearly shows that a single and large posterior interior alveolar foramen is located above the tenth tooth position. The tooth crowns on this specimen are not well-preserved, but are similar in shape to those of UALVP 29892.

The other three specimens (UALVP 29893-29895) are less well preserved than the two described above, in terms of showing the general shape of the maxillary. However, UALVP 29894 is significant, because the four teeth on this specimen show slightly recurved crowns with faint medial, but no lateral striations, consistent with the posterior dentary teeth described above. This specimen also shows a prominent palatine process closely associated with a single large posterior interior alveolar foramen (also shown in UALVP 29895).

Discussion: The holotype described above from the Oldman Formation represents a new, Judithian species of Odaxosaurus, which differs principally from the Lancian O. piger in having a more robustly built dentary with fewer, less truncate teeth, and a less well-developed intramandibular septum extending anteriorly to the midpoint of the tooth row. Referred specimens from the same formation show other taxonomically significant charater states for the new species, including the possession of a more prominent premaxillary process of the maxillary, and tooth crowns having much weaker medial striations (while no lateral striations are shown on the specimens of O. priscus). O. priscus is clearly on the glyptosaurine line of evolution, as evidenced by its close resemblance in dentary structure and tooth morphology to the Lancian Odaxosaurus piger, which is currently regarded as a precusor of the Tertiary true glyptosaurines (Estes 1983a; Sullivan 1986a-b). The dentary of this Judithian form has a shallow but anteriorly extending intramandibular septum, and obtuse teeth with faint medial striations, from which the Lancian O. piger can be easily derived. Therefore, the Judithian species represents the earliest known stage in glyptosaurine evolution. There are no osteoscutes directly associated with O. priscus (e.g., fused to the maxillary or dentary specimens), but the discovery of advanced glyptosaurine-type of osteoscutes from the Judithian deposits in New Jersey (Denton et al. 1991) indicates that the splitting of glyptosaurines from their ancestral group can be traced at least back to Judithian time.

Several authors have referred specimens of Judithian age to the Lancian species Odaxosaurus piger. But this study shows that these referrals are either erronous or unconvincing: Sahni (1972: 354) referred two specimens (AMNH 8494-8495) from the Judith River Formation to "Peltosaurus piger" (now Odaxosaurus piger) on the characters that are symplesiomorphic for the family Anguidae (e.g., "anteriorly the Meckelian fossa is ventral in position" and "intramandibular septum .... originates slightly anteroventral to the notch of the internal mental foramina"). To Sahni's referral of these two specimens to Odaxosaurus piger, I here offer the following comments: 1) AMNH 8494 (Sahni 1972, fig. 8H), an incomplete right dentary with all the teeth broken off, is certainly an anguid as it shows a notched tooth-bearing border in combination with the loss of the sulcus dentalis and subdental shelf. However, it differs from the dentary of Odaxosaurus in having a straight tooth-bearing border, and more importantly, having cylindrical but not transversely expanded tooth shafts (as evidenced by their broken bases). Similar materials are also known from the Oldman and the Milk River formations, which are identified as "Anguidae, genus & species undetermined" in this paper. 2) AMNH 8495 (Sahni 1972, fig. 8G) as described appears to be referrable to Odaxosaurus, as Sahni (1972: 354) stated that "the teeth are pleurodont, linguolabially expanded, and the transverse width is only slightly smaller than the height. The crown is expanded relative to the shaft and consists of a distinct anteroposteriorly directed crest rather than separate cuspules." However, the clear figure of the specimen (Sahni 1972, fig. 8G) contradicts this description, and indicates that it is largely artificial. In fact, all but one tooth on the maxillary are broken off, and the one preserved is slender, definitely neither chisel-shaped nor striated. Therefore, this specimen should be excluded from Odaxosaurus. It seems to me that Sahni's figure shows a Contogenys-like lizard, which is comparable to UALVP 29830 from the Milk River Formation (see foregoing description).

Estes (1983a) referred several specimens from the "Mesaverde" Formation in Wyoming to the species Odaxosaurus piger, in his monographic review of fossil lizards. Without a description or figure, it is difficult to evaluate the reliability of this identification.

Anguidae, genus & species undetermined

Plate 13, Figs. 11-12

Referred specimens: UALVP 33378, incomplete left dentary from MR-4 locality; UALVP 33379, fragmentary left dentary from MR-6 locality; and many unnumbered maxillary and dentary fragments from MR-4, MR-6, MR-8 and MR-20 localities.

Locality and horizon: MR-4, MR-6, MR-8, and MR-20 localities, Verdigris Coulee, approximately 30 km east of the village of Milk River, southern Alberta; upper member of the Milk River Formation (early Campanian or Aquilan in age), Upper Cretaceous.

Description: UALVP 33378 consists of the middle and posterior part of a small left dentary, bearing six teeth and vacant positions for two others. Medially, the subdental shelf is greatly reduced as a smoothly sloped tooth-bearing border, which is posteriorly notched for the anterior inferior alveolar foramen. The Meckelian canal anterior to the notch cannot be seen from the medial view; however, a ventral view shows that the canal is greatly restricted opening ventrally throughout most of its length as a shallow and narrow gutter. A slightly flattened ventral surface of the tooth-bearing border anterior to the notch indicates that a greatly reduced splenial terminated anteriorly close to the midpoint of the tooth row. Posteriorly within the Meckelian canal, a small but clearly defined intramandibular septum is vertically directed; it has a free ventral border, and is posteriorly notched for the Meckelian cartilage (Plate 13, Fig. 11).

The dentary teeth are high-crowned, having a cylindrical shaft and a small basal foramen opening medially at the tooth base. Most of the teeth have the crowns broken off, but two are well preserved and show that the crowns may have faint medial striations. These teeth are pleurodont, having one-third of tooth height projecting above the well-developed lateral parapet of dentary.

The lateral surface of the dentary is smooth, lacking any sculpture. Three inferior alveolar foramina preserved on the specimen are large, open anterolaterally, and aligned horizontally about the midway in the height of the dentary. These foramina are more or less equally spaced from one another.

A more fragmentary dentary of this kind is known from a second locality, MR-6. UALVP 33379 shows the same jaw construction and proportions as the above-described specimen: the size, notched tooth-bearing border, and well-developed intramandibular septum, match UALVP 33378 and allow both to be referred to the same species.

On the basis of similar jaw construction and proportions, several unnumbered fragmentary maxllaries and dentaries in the Milk River collection are also referrable to this taxon. These specimens were collected from MR-4, MR-6, MR-8, and MR-20 localities.

Discussion: R. C. Fox (in sch.) made the original identification of the above-described specimens as Anguidae. As a result of this study, his placement of these specimens in the Anguidae is supported by a well-established synapomorphy: the dentary tooth-bearing border is notched for the anterior inferior alveolar foramen, so that the dentary forms the dorsal and anterior border of the foramen (Estes 1964; Estes et al. 1988). These specimens also show synapomorphies for a higher taxon, Anguimorpha; these include: a Meckelian canal that opens ventrally anterior to anterior inferior alveolar foramen (Estes 1964; Estes et al. 1988); a posterior part of the Meckelian canal that is subdivided by a vertically directed intramandibular septum (ibid.). These specimens also show a great reduction of the subdental shelf corresponding with the total loss of sulcus dentalis, as commonly seen in other anguimorphans.

Although undetermined at generic and specific levels, the identification of these specimens as Anguidae (Fox in sch.) is significant, as these early Campanian materials document the undoubtedly earliest record for this family, whereas the Commanchean "Anguidae?" (Winkler et al. 1990) is probably a scincomorphan instead (see later discussion on Anguidae).

Family Necrosauridae Hoffstetter 1943

Genus Colpodontosaurus Estes 1964

Type species: Colpodontosaurus cracens Estes 1964.

Range: Upper Cretaceous, North America.

Diagnosis: As for the type and only known species.

Colpodontosaurus cracens Estes 1964

Plate 14, Figs. 1-3

Holotype: UCMP 46608, an incomplete left dentary having broken bases for three, and vacant spaces for 12, dentary teeth. The holotype was figured by Estes (1964, fig. 60) with several teeth restored from other specimens.

Referred specimens: UALVP 33388, fragmentary left dentary from the KUA-3 locality, Scollard Formation, Alberta. In addition, some specimens from outside the study area are also included in this paper, because they show significant individual variation within the species. These specimens are: UALVP 29781-29784, incomplete dentaries from the BTB locality, Lance Formation in Wyoming; UALVP 29785-29786, fragmentary dentaries from the BCA locality, Hell Creek Formation in Montana.

Known distribution: Upper Cretaceous Lance Formation, eastern Wyoming; Hell Creek Formation, eastern Montana; and Scollard Formation, central Alberta.

Diagnosis (revised from Estes 1983a): A Late Cretaceous necrosaurid lizard differing from Provaranosaurus Gilmore 1942a, its closest known relative, in having a more slender jaw, lower crowned and nonstriated teeth, and a small ventral process on the weakly developed intramandibular septum.

Description: UALVP 33388 is the only specimen of this species collected from the Scollard Formation. The fragmentary left dentary bears a broken tooth and the vacant spaces for three others. Like the specimens from the Lance and Hell Creek formations, this dentary shows taxonomically significant features: the subdental shelf (without sulcus dentalis) is in a very low position; the tooth base is expanded, lacks striations, and has a basal foramen opening posteromedially; the teeth are hollow and have strongly constricted and possibly recurved crowns (comparing UALVP 33388 with UALVP 29782, see Plate 14, Figs. 1, 3). The size and robustness of this dentary compared to those from the Lance and Hell Creek formations indicate that the Scollard specimen is probably from a relatively old individual.

Among the several specimens of C. cracens from the BTB locality in the UALVP collections, UALVP 29781 is relatively complete, with only the anterior end missing. The dentary shows the same general configuration as the holotype of the species, but differs from the latter in having four (rather than two) inferior alveolar foramina on its lateral surface, although it is smaller than the holotype. There are no teeth preserved on the specimen, but 13 tooth positions can be clearly seen. The total number of dentary teeth for this lizard is estimated as close to 20, as in the holotype.

Another specimen, UALVP 29782, consists of the posterior part of a right dentary, including the most posterior eight tooth positions. This dentary has three incomplete teeth preserved, showing that the tooth bases are slightly expanded, nonstriated, and each bears a small basal foramen. The tooth crowns are greatly constricted, and are obviously less recurved than those Estes (1964) figured for the holotype. The development of the intramandibular septum is similar to that of the holotype and the other specimens included in this collection in lacking a free ventral border but bearing a tiny ventral process.

Discussion: The Lancian Colpodontosaurus cracens was originally diagnosed by Estes (1964) as a lizard having thin-walled, pointed, recurved, and short teeth; and having a tiny free ventral process of the intramandibular septum. The specimens in the UALVP collections from the Lance and Hell Creek formations provide no new information relevant to the diagnosis of this lizard, but show some variation in the curvature of the dentary teeth and the number of inferior alveolar foramina. Estes (1964, fig. 60) figured the holotype with strongly recurved teeth (restored from other specimens, according to Estes), while UALVP 29782 shows that the teeth have a relatively straight shaft with only the tip of the crown slightly recurved. The holotype, as Estes (1964) described, has only two inferior alveolar foramina on its lateral surface, while UALVP 29781 (also UALVP 29785) shows four foramina. Recognition of these variations is significant for a better understanding of this species.

Estes (1964) originally placed Colpodontosaurus cracens in the Diploglossa (=Anguidea) incertae sedis, on the basis of the tiny ventral process of the intramandibular septum, absence of basal infoldings of the teeth, and the presumed lack of an intramandibular hinge. More recently, Estes (1983a), referred C. cracens to the Necrosauridae on the basis of resemblances in jaw and tooth structure to some necrosaurids (e.g., lack a free ventral border of the intramandibular septum as in necrosaurids generally; thin-walled teeth as in Provaranosaurus). This familial placement is followed in this paper. However, it should be noted that C. cracens is based on dentary materials (in most cases on specimens with the teeth broken off), and maxillary and other skull elements are unknown or poorly known as yet. A better understanding of the relationships of this lizard at and below the familial level depends on further study of better preserved materials.

Genus & species new (unnamed)

Plate 14, Figs. 4-5

Referred specimens: UALVP 29787, 33383; both right dentaries with several broken teeth.

Locality and horizon: MR-6 locality, Verdigris Coulee, approximately 30 km east of the village of Milk River, southern Alberta; upper member of the Milk River Formation (Aquilan in age), Upper Cretaceous.

Known distribution: Upper Cretaceous Milk River Formation, southern Alberta, Canada.

Description: UALVP 29787 is a short, slender, and delicate dentary (7 mm long as preserved) that abruptly tapers anteriorly and ends at a weak mandibular symphysis. The lateral surface of the dentary is smooth and much less convex than that of *Colpodontosaurus cracens*. As in the latter species, the anteroventral edge of the dentary turns sharply medially, forming part of the floor of Meckelian canal. Four inferior alveolar foramina (mental foramina) are small, and unequally spaced from one another.

Medially, the dentary bears a delicately built but prominent subdental shelf, which is nearly equal in thickness along its extent; in *Colpodontosaurus cracens*, the shelf is much less developed and thins posteriorly. The sulcus dentalis is absent in this specimen, as in *Colpodontosaurus cracens*. The Meckelian canal narrows sharply anteriorly, and turns ventrally. There is no groove beneath the subdental shelf for the splenodentary articulation, but the ventral edge of the dentary bears an articular surface for the splenial, indicating that it extended anteriorly to about the midpoint of the tooth row, leaving a long and ventral opening of the Meckelian canal anteriorly. As seen in *Colpodontosaurus cracens*, the intramandibular septum lacks a free ventral border, but bears a small ventral process, which is much less prominent than that of Colpodontosaurus cracens.

The preserved portion of the dentary bears broken bases and spaces for 13 teeth. The four tooth bases that are preserved show that the teeth are short and thin-walled, and have swollen and nonstriated bases. The dentary tooth row is incomplete, but can be estimated as having about 16 positions, significantly fewer than that in Colpodontosaurus cracens. Every tooth has a small, circular basal foramen, which is medioposterior in position at the tooth bases.

Another specimen (UALVP 33383), also a right dentary from the MR-6 locality, has one tooth and the broken bases for seven others preserved. This specimen is slightly bigger and stronger than UALVP 29787, but it can be referred to the same species on the basis of thin-walled teeth and a wide but slender subdental shelf.

Discussion: The two specimens (UALVP 29787, 33383) are referrable to the Necrosauridae, on the basis of their general tooth morphology and dentary structure (e.g., thin-walled teeth lacking basal striations, poorly developed intramandibular septum). Although the two dentaries are not well-preserved, the significance of this discovery is obvious, as the specimens document the earliest fossil record of the Necrosauridae in North America, and represent an Aquilan species that was closely related to the Lancian Colpodontosaurus cracens (Fox [1972] recognized this relationship by identifying UALVP 29787 as "Colpodontosaurus? sp."). The Milk River specimens share with the Lancian Colpodontosaurus cracens thin-walled, low-crowned, and nonstriated teeth, and a tiny ventral process on the weakly developed intramandibular septum; but differ from the latter (at the generic level) in having a short dentary with a prominent subdental shelf. These morphological differences, combined with 18 Myr geological time gap between Milk River and Lance horizons, suggest that the Milk River form represents a new genus and species;

however, the new taxon is not named in this paper, because the two specimens described above are too poorly preserved for an adequate diagnosis for a new genus and species.

Genus Parasaniwa Gilmore 1928

Type species: Parasaniwa wyomingensis Gilmore 1928.

Range: Upper Cretaceous, North America.

Diagnosis: As for the type species.

Parasaniwa wyomingensis Gilmore 1928

Plate 14, Figs. 6-12

1928 Parasaniwa obtusa Gilmore, pl. 26, figs. 10, 12

Holotype: USNM 10797, fragmentary left dentary having one complete and two broken teeth, collected by J. B. Hatcher in 1892 from the Lance Formation, eastern Wyoming (see Gilmore 1928; Estes 1964, 1983a).

Referred specimens: Frenchman Formation, Wounded Knee locality: UALVP 33347, premaxillary with two teeth; UALVP 33348, right maxillary fragment with two teeth; UALVP 33349, incomplete left dentary having ten tooth positions; UALVP 33350, dorsal vertebra.

Scollard Formation, KUA-1 locality: UALVP 33384, fragmentary maxillary with two teeth.

Lance Formation, BTB locality: UALVP 33351-33353, incomplete tooth-bearing maxillaries; UALVP 33354, frontal; UALVP 1612, 1616, 33355-33356, incomplete tooth-bearing dentaries.

Hell Creek Formation, BCA locality: UALVP 33357-33360, tooth-bearing maxillary fragments; UALVP 33361, and several unnumbered dentaries; UALVP 33362-33363, toothed pterygoids; UALVP 33364-33365, parietals.

Known distribution: Upper Cretaceous Lance, Hell Creek, Frenchman, and Scollard formations, all Lancian in age. Congeneric specimens are also known from the Oldman Formation (Judithian in age), southern Alberta (see later description and discussion).

Diagnosis (revised from Estes 1983a): Late Cretaceous necrosaurid lizard from North America, differing from Necrosaurus Filhol 1876 in having skull osteoscutes fused, flattened, and separated by shallow and wide grooves; maxillary having higher and vertically-directed dorsal process, which rises abruptly behind narial opening; marginal teeth strongly compressed laterally, trenchant, but lacking serrations; tooth bases dilated and having pronounced basal striations.

Description: Gilmore (1928) gave an excellent description of the holotype dentary from the Lance Formation. Estes (1964) revised the description of the dentary on more nearly complete specimens, and for the first time described and figured maxillary, frontal and parietal materials of this species from the same formation. The following description focuses on the specimens in UALVP collections, especially on those from the Scollard and Frenchman formations, central Alberta and southwestern Saskatchewan, where the newly discovered specimens indicate a northern extension of the geographical distribution of this species. Other specimens from the BTB and BCA localities are included in this study as comparative materials from the same horizon but different geological formations.

Premaxillary.-UALVP 33347 from the Wounded Knee locality, Frenchman Formation, is the first premaxillary specimen to be described for Parasaniwa wyomingensis. The premaxillary is a single unit (unpaired), having five tooth positions. Two poorly preserved teeth show basal infoldings, the same tooth form as seen in the maxillary and dentary specimens. Dorsally, the premaxillary spine is tall, splint-like, and slightly recurved in correspondence with the high postnarial process of the maxillary. On each side of the base of this spine are two well-defined premaxillary foramina, through which passed nerves and blood vessels to the bases of the premaxillary teeth. Although no osteoscutes are shown on the premaxillary, this specimen is different from the premaxillary of Paraderma in having a narrow and tall splint-like spine, and lacking a plate-like palatal process; and it is too small to pertain to Palaeosaniwa. Therefore, this specimen is here referred to Parasaniwa.

Maxillary.-UALVP 33384 consists of a fragmentary tooth-bearing right maxillary from the Scollard Formation, central Alberta. The two teeth preserved in front of the posterior interior alveolar foramen are short, strongly trenchant, but have no serrations on their anterior and posterior blades. The tooth bases are strongly expanded and striated with basal infoldings (Estes 1964 noted that the degree of these striations is individually variable within the species). The supradental shelf is flat and horizontal, lacking a dorsal fold, and the lateral wall of the maxillary is thin and clearly lacks thick osteoscutes, in these aspects differing from the maxillary of Paraderma (see later description). Other maxillaries from the Frenchman, Lance, and Hell Creek formations numbered above are referred to Parasaniwa wyomingensis on the basis of their tooth form and/or sculpture pattern on the lateral surface of the maxillaries.

Dentary.-Among the dentary specimens referred to this species, two (UALVP 33349, 33361) are more extensively preserved than others. UALVP 33349 is a left dentary from the Wounded Knee locality, Frenchman Formation. The specimen as preserved has ten tooth positions, including four teeth and the bases as well as spaces for six others, These teeth are pleurodont (in contrast to Estes' [1964] "subpleurodont"), as only half or less of the tooth height projects above the lateral parapet of the jaw. The dentary shows the same configuration and structure as does UCMP 46041, a nearly complete dentary from the Lance Formation (see Estes 1964, fig. 61): it is slender, lightly built, has a delicate symphyseal process, and a crescentic tooth-bearing border (see Estes 1964: 129). However, the Frenchman dentary is much smaller and more slender than UCMP 46041, indicating that it is from a young individual.

The other dentary (UALVP 33361), also from the left side, is from the BCA locality, Hell Creek Formation. This specimen reinforces Estes' statement that "the intramandibular septum is fused to the floor of the Meckelian groove throughout its length, and has a small notch posteriorly for Meckel's cartilage" (Estes 1964: 129); and, together with other specimens (UCMP 46041, UALVP 1612), shows that the groove for the anteromedial process of the coronoid bone is developed below the last four tooth positions, where the tooth-bearing border suddenly becomes narrow.

Frontal.-UALVP 33354 and another unnumbered specimen are clearly referrable to this species, as they show the same osteoscute pattern as the parietals of P. wyomingensis (see Estes 1964). UALVP 33354 is a right frontal broken away from the left side at the midline. The unnumbered frontal from the same locality is similarly preserved. Estes (1964) described a fused frontal (AMNH 8103) with the midline suture clearly visible ventrally. Discovery of the new specimens from the BTB locality (Lance Formation) indicates that fusion of the frontals is an ontogenetic character for this lizard.

Parietal.-Two specimens (UALVP 33364-33365, both from the BCA locality) are identified as parietals of Parasaniwa wyomingensis: they are closely similar to UCMP 54200 (Estes 1964, fig. 63), a well-preserved parietal from the type Lance Formation. Although the two parietals are poorly preserved both in terms of completeness and sculpture pattern, their general shape, size, and especially the lateral flange for the temporal musculature indicate that they belong to the same species as UCMP 54200.

Pterygoid.-Two small pterygoid fragments, UALVP 33362-33363 from the BCA locality, are referrable to Parasaniwa wyomingensis. Both of the specimens are too small and slender to be referrable to Paraderma or Palaeosaniwa, but are consistent with the maxillaries and dentaries referred to Parasaniwa wyomingensis from the same locality. Both specimens show that the pterygoid of this lizard is toothed, a primitive character state. UALVP 33362-33363 are not only different from UALVP 33338 (a pterygoid referred to Palaeosaniwa, see later description) in size and robustness, but more importantly, in them the pterygoid teeth are arranged along the medial border of the palatine process (in UALVP 33338 there are no teeth on the medial border of the pterygoid).

Vertebra.-UALVP 33350 and several unnumbered vertebrae from the Wounded Knee locality are referrable to Parasaniwa wyomingensis. UALVP 33350 is a well-preserved dorsal vertebra, which is clearly different from that of Palaeosaniwa in having a much weaker diapophysis below the prezygapophysis, and in having a much less constricted condylar base. In addition, UALVP 33350 and several unnumbered specimens are obviously too small to be referrable to Palaeosaniwa or Paraderma; they are consistent in size with the jaw materials for Parasaniwa.

Discussion: The taxonomic history of Parasaniwa is short and straightforward, compared to several other Cretaceous lizard taxa. Based on fragmentary dentary material from the Lance Formation, Gilmore (1928) founded Parasaniwa, and designated P. wyomingensis as the type species. His Parasaniwa included another species, P. obtusa, from the same locality. He separated the latter species from the type species on the basis that "it differs from the single complete tooth known of P. wyomingensis from the same formation and locality in having an erect crown (not recurved) with an obtusely pointed apex, and with striations restricted to the extreme basal surfaces" (Gilmore 1928: 86). Estes (1964) correctly placed P. obtusa in synonymy with P. wyomingensis, as he confirmed by personal observation that the obtuse crown of P. obtusa is the result of erosion, and the degree of basal striations is variable for this lizard. A comparison of a large number of specimens in the UALVP collections shows that larger individuals have stronger basal striation than the smaller ones, indicating that this variation is an ontogenetic character. Here, I add another point in support of Estes' revision: the maxillary that Gilmore placed in *Parasaniwa obtusa* (USNM 10800; Gilmore 1928, pl. XXVI, fig. 10) shows obviously stronger basal striations than his holotype dentary (USNM 10798), and is indistinguishable in structure from those later referred to *P. wyomingensis* (see Estes 1964, and the present paper). Therefore, both the holotype and the included specimens for Gilmore's *Parasaniwa obtusa* should be referred to the type species, and *P. obtusa* should be regarded as a junior synonym of *P. wyomingensis*.

The familial assignment of *Parasaniwa* has been changed since Gilmore's original description in 1928. Gilmore (1928) originally placed *Parasaniwa* in the family Varanidae, but noted its striking similarity in tooth form to *Palaeovaranus cayluxi* Filhol 1877 (= *Necrosaurus cayluxi* Filhol 1873, see Estes 1983a). Later, McDowell and Bogert (1954: 32) accepted Gilmore's familial designation of *Parasaniwa* as a saniwine varanid, but noted that "there is a suggestive similarity in dental form between *Exostinus lancensis* and its contemporaries and compatriots *Parasaniwa obtusa* and *P. wyomingensis*." In fact, a trenchant crown pattern is a generalized character state shared by many carnivorous anguimorphans. Estes (1964) erected a new family, Parasaniwidae, which includes both *Parasaniwa* and *Paraderma*, and diagnosed the family as including genera that are "characterized by teeth with simple basal fluting extending into the medullary cavity; development of an intramandibular jaw hinge; unretracted nares; skull roof with well-defined scute areas; scutes tending toward multiplication" (Estes 1964: 128). Later, Hoffstetter (1969) recognized the close relationships between Parasaniwidae and Necrosauridae on the evidence from maxillary structure and skull osteoscutes, and suggested that the differences between the two groups are not great enough to separate them at a familial level. Accepting Hoffstetter's interpretation and on more extensive discussion with other collegues, Estes (1983a) synonymized his Parasaniwidae with Necrosauridae Hoffstetter 1943, and tentatively allocated *Paraderma* to the Helodermatidae Gray 1837 (see later discussion on *Paraderma*).

The new specimens from several localities at Lancian horizons add no new information concerning the familial affiliation of this lizard; thus, in this paper Parasaniwa wyomingensis remains as a Cretaceous necrosaurid as Estes (1983a) classified it.

The geologic distribution of the species Parasaniwa wyomingensis, in our current understanding, is limited to Lancian horizons. The specimens of this particular species were previously known from the Lance and Hell Creek formations (Gilmore 1928; Estes 1964; Estes et al. 1969), and now from the Frenchman and Scollard formations (Fox 1989; and this paper). Post-Lancian Parasaniwa sp. has been reported by Hecht (1959) from Eocene deposits in Wyoming, and by McKenna (1960) from the Eocene of Colorado. However, these Eocene materials are likely belong to another genus (Estes 1983a); accordingly, the Eocene record of Parasaniwa is rejected. Pre-Lancian congeneric materials have been reported in a faunal list from the Oldman Formation of Alberta (Fox 1976; Currie 1986; Eberth 1987; Koster et al. 1987), but these Judithian materials likely represent another species (see following description and discussion).

Three fragmentary specimens (UALVP 33923-33925) from the Milk River Formation are Parasaniwa-like, as they have laterally compressed teeth with trenchant cutting blade and weak basal infoldings. However, these specimens are poorly preserved and are not definitely referrable to Parasaniwa; they are identified as "?Parasaniwa sp." (see Plate 15, Figs. 10-12).

Parasaniwa n. sp. (cf. *P. wyomingensis*)

Plate 15, Figs. 1-9; Text-fig. 22

Specimens: UALVP 33346, 33366-33369, RTMP 65.24.6, 81.38.4, and 27 unnumbered specimens, all incomplete maxillaries; UALVP 33370-33373, RTMP 79.8.631, and more than 30 unnumbered fragment specimens, all dentaries; UALVP 33374, frontal; UALVP 33375-33376, RTMP 82.20.36, 84.168.2, parietals.

Locality and horizon: The specimens listed above are collected from various localities of the Upper Cretaceous Oldman Formation, southeastern Alberta, Canada; the UALVP specimens are from the Irvine locality; and the RTMP specimens are from the Railway Grade, White Rock Coulee, Hope Johnson's Microsite (DPP), Sandy Point, and Manyberries localities (coordinate see following description of each specimen).

Description: All the specimens listed above can be distinguished from those referred to *Palaeosaniwa* or *Paraderma*, and can be recognized as *Parasaniwa*-like on the basis of general jaw proportions, tooth form, or texture of osteoscutes. Several relatively well-preserved specimens are described as follows.

Maxillary.-UALVP 33346 is a nearly complete right maxillary from the Irvine locality, Oldman Formation. In proportions and sculpture pattern generally this specimen is *Parasaniwa*-like, but differs from that of the type species (*P. wyomingensis*) in having a roughly triangular dorsal process (see Plate 15, Figs. 1-2) and a greater number of tooth positions anterior to the posterior interior alveolar foramen (seven vs. six for *P. wyomingensis*). Anteriorly, the two premaxillary processes are short and are not clearly separated from each other, because the notch between them is poorly developed. The anterior interior alveolar foramen is small, rounded, and opens entirely on the internal side of the nasal process, so that it is clearly visible in medial view. The nasal process (= the dorsal or facial process of other authors) rises behind the narial opening at about a 45 degree angle, then curves along a gentle slope associated with the inward bending of the dorsalmost part of the process (there is seems to be no such step in UCMP 49935 if Estes' (1964) reconstruction is correct). The posterior border of the nasal process declines at a similar angle, giving the entire process a roughly triangular shape. UALVP 33346 is so far the most nearly complete maxillary known for Parasaniwa and is the best preserved with respect to the texture of the osteoscutes. The lateral surface of the nasal process is vertically oriented, except for the medial curvature dorsally. The surface above the superior alveolar foramina is extensively covered with osteoscutes that are fused to the bone beneath. These osteoscutes are thin, flat, and have a vermiculate sculpture (see Plate 15, Fig. 1). The superior alveolar foramina, as many as eight, are small and open anteroventrally.

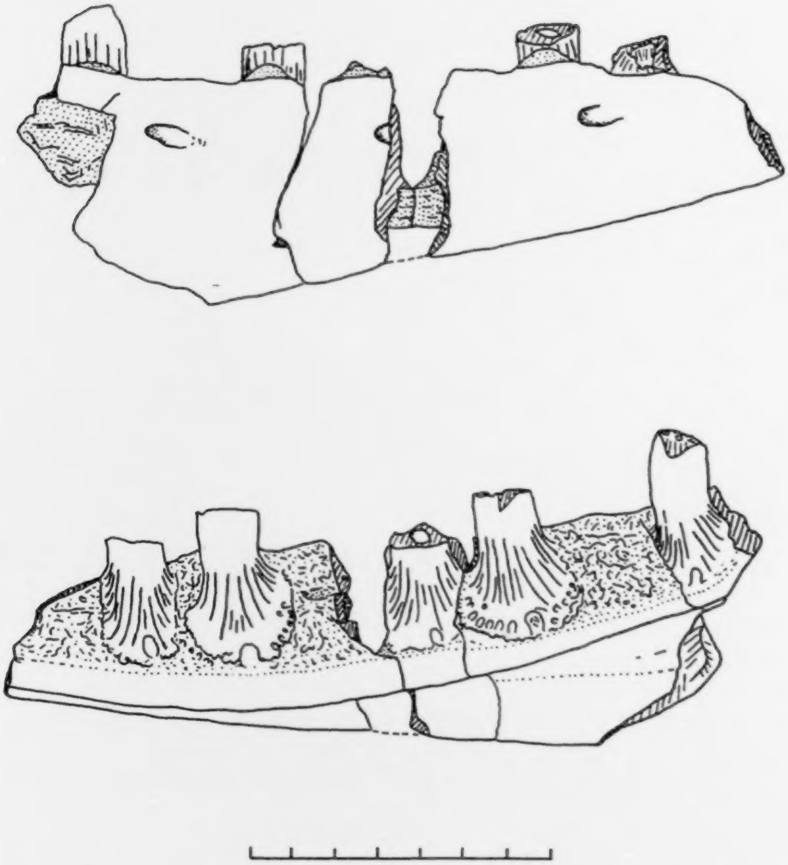
Internally, the maxillary bears a well-preserved supradental shelf, which is a flat, shelf-like structure lacking the thickening (fold) seen in Paraderma. Above the shelf and internal to the lateral wall of the maxillary is an elongated notch (or depression) for the nasal cavity, which extends to the midpoint of the maxillary tooth row. A large foramen (posterior interior alveolar foramen) opens above the eighth tooth position, and a small anterior interior alveolar foramen opens medially above the second tooth as described before. This specimen shows eight tooth positions, including the bases of five and the spaces for three others. The tooth bases have simple and short basal infoldings as in the Lancian Parasaniwa wyomingensis. The posterior end of the maxillary is broken, so that the total number of maxillary teeth is unknown; but it can be estimated as 11-12, since four or five positions are often seen along the tooth row posterior to the posterior interior alveolar foramen.

RTMP 81.38.4 is the fragment of a right maxillary from the White Rock Coulee (Sec. 16, Tp. 17, R 3, W 4), about 50 km north of Medicine Hat. The fragment shows one complete tooth, which is trenchant and slightly recurved, as in Parasaniwa wyomingensis

(UALVP 33368 from the Irvine locality shows the same type of tooth form). This maxillary fragment also shows that there are at least four positions for the tooth row behind the posterior interior alveolar foramen.

Dentary.-Among the dentaries referred to this species, two specimens from the Irvine locality (UALVP 33370-33371) are better preserved than the others. UALVP 33370 consists of the posterior half of a left dentary, which is broken directly in front of the sixth tooth position from the rear. This specimen is important as it shows that the intramandibular septum of Judithian *Parasaniwa* remains fused to the floor of the Meckelian canal through most of it length, with only the very posterior end having a tiny separation. This is the same condition as seen in Lancian specimens, indicating that there has been no change in this aspect of jaw structure for the approximately 11 Myr. known for the evolution of *Parasaniwa*. However, the tooth-bearing border of the Judithian species is much less crescentic than that in the Lancian *P. wyomingensis*. UALVP 33370 has four tooth bases and the spaces for two others. The tooth bases show the simple basal infoldings as in the Lancian specimens. The lateral surface of the dentary is smooth, and is more nearly flat than convex. The last inferior alveolar foramen opens lateral to the third most posterior tooth position.

Another specimen, UALVP 33371, is an even better preserved right dentary, but the intramandibular septum is broken. The tooth bases have the same kind of infoldings as UALVP 33370, but these are stronger, as this is a larger specimen from a presumably older individual. On four of the teeth the crowns are broken, but one (second to last of the complete tooth row) is nearly complete. This tooth has strongly trenchant, blade-like cutting edges, but no serrations can be seen on the edges. These dentary teeth are pleurodont, having the lower half of the tooth height attached to the high lateral parapet of the dentary.



Text-fig. 22. Necrosauridae, *Parasaniwa* n. sp. (cf. *P*. *wyomingensis*), Oldman Formation, southeastern Alberta; UALVP 33371, incomplete right dentary; (above) lateral view, (below) medial view. Scale = 5 mm.

Frontal.-UALVP 33374 from the Irvine locality is a fragmentary right frontal referred to Parasaniwa on the basis of its thin, large patches of osteoscutes. Once again, this specimen shows that the frontals of Parasaniwa are paired, and the fused condition (Estes 1964) is likely an ontogenetic character. On the ventral side of the frontal, the subolfactory process (flange) is well developed, but seems not to meet at the ventral midline.

Parietal.-Four parietals from the Oldman Formation are referrable to this Judithian species on the basis of the general shape of the parietal table and the osteoscute pattern; these include UALVP 33375-33376 from the Irvine locality, RTMP 82.20.36 from the Railway Grade, and RTMP 84.168.2 from Sandy Point (Sec. 34, Tp. 21, R 1, W 4). All four specimens have the parietal table well-preserved, but the temporal process is broken. These specimens together indicate that the parietal of this Judithian species is similar to that of Lancian Parasaniwa wyomingensis in general proportions and osteoscute pattern, but differs from the latter in having both the parietal foramen and the parietal fossa in a more posterior location and the fused osteoscutes covering only the anterior half of the parietal table.

Discussion: The specimens described above represent a Judithian lizard that is referrable to Parasaniwa, as they show close resemblances to the type species, Parasaniwa wyomingensis, in general jaw proportions, tooth form, and osteoscute pattern. However, this Judithian form differs from the type species in having a roughly triangular dorsal process of maxillary, less crescentic tooth-bearing border of dentary, a more posterior location for the parietal foramen, and in having a less extensive covering of fused osteoscutes on the parietal. The foramen in the Judithian specimens is close to the centre of the parietal table, while that on the Lancian specimens (e.g., UCMP 54200) is close to the frontoparietal suture; the fused osteoscutes on the Judithian specimens cover only the anterior half of the parietal table, while those on the Lancian specimens cover two-thirds or more. These differences are so consistent on all the four specimens in the collection that they cannot be regarded as individual variations (or sexual dimorphism). Instead, the morphological differences plus the difference in geologic age (middle Campanian vs. late Maestrichtian) suggests that a more primitive species is represented here. However, I am unable to name this new species at present, because all the dentaries known for this species are too fragmentary to be comparable to the holotype of P. wyomingensis; similarly, the new species is represented by well-preserved maxillary material, while in Lancian P. wyomingensis the maxillary is poorly known. Discovery of a better preserved dentary may reveal more significant diagnostic characters for this new species.

Family Helodermatidae Gray 1837

Genus Paraderma Estes 1964

Type species: Paraderma bogerti Estes 1964.

Range: Upper Cretaceous, North America.

Diagnosis: As for the type species.

Paraderma bogerti Estes 1964

Plate 16, Figs. 1-14; Text-figs. 23-24

Holotype: UCMP 54261, incomplete left maxillary from the Lance Formation, Niobrara County, Wyoming (see Estes 1964).

Referred specimens: Scollard Formation, KUA-1 locality: UALVP 29845, and several unnumbered specimens, tooth-bearing dentaries; UALVP 33385, incomplete parietal; UALVP 33902-33910, disarticulated cervical and dorsal vertebrae. Frenchman Formation, Wounded Knee locality: UALVP 29846, incomplete right dentary; and UALVP 33387, dorsal vertebra.

Known distribution: The Upper Cretaceous Lance Formation, eastern Wyoming; Hell Creek Formation, eastern Montana; Scollard Formation, central Alberta; and Frenchman Formation, southwestern Saskatchewan; all Lancian (Maestrichtian) in age. Pre-Lancian distribution of the species is reported from the Judith River Formation (Sahni 1972), but see later discussion.

Diagnosis (revised from Estes 1983a): A Late Cretaceous helodermatid from North America, differing from other fossil and Recent forms of the same family by a combination of the following character states: marginal teeth robust, with less conspicuous venom groove; parietal foramen present; cephalic osteoscutes polygonal, with pitted sculpture and separated by wide groove; neural spines on trunk vertebrae vertically directed.

Description: Several specimens in UALVP collection from the KUA-1 locality provide significant material for a better understanding of Paraderma bogerti. The specimens described below include parietal, vertebrae, and limbbones that are the first known for this species, and a well-preserved dentary bearing teeth with a venom groove.

Dentaries.-Among the dentaries referred to Paraderma bogerti in this paper, two are well-preserved. The first, UALVP 29845, is a left dentary from the KUA-1 locality, the Scollard Formation, central Alberta. The specimen is anteriorly complete, having the symphysial part well-preserved, but is broken posteriorly at the tenth tooth position. Nevertheless, it is the best dentary specimen known for this species. Anteromedially, the dentary bears a prominent symphysial process, corresponding with the strong medial curvature of the jaw and making the mandibular arch widely U-shaped. The subdental shelf and the sulcus dentalis are entirely absent; instead, a robust and relatively straight tooth-bearing border forms most of the medial side of the Meckelian canal. The anterior half of the Meckelian canal opens ventrally, but the posterior half gradually turns ventromedially in correspondence with the posterior deepening of the jaw. Because of the breakage at the tenth tooth position, the nature of the intramandibular septum cannot be determined from this specimen (but see the description of the second specimen below).

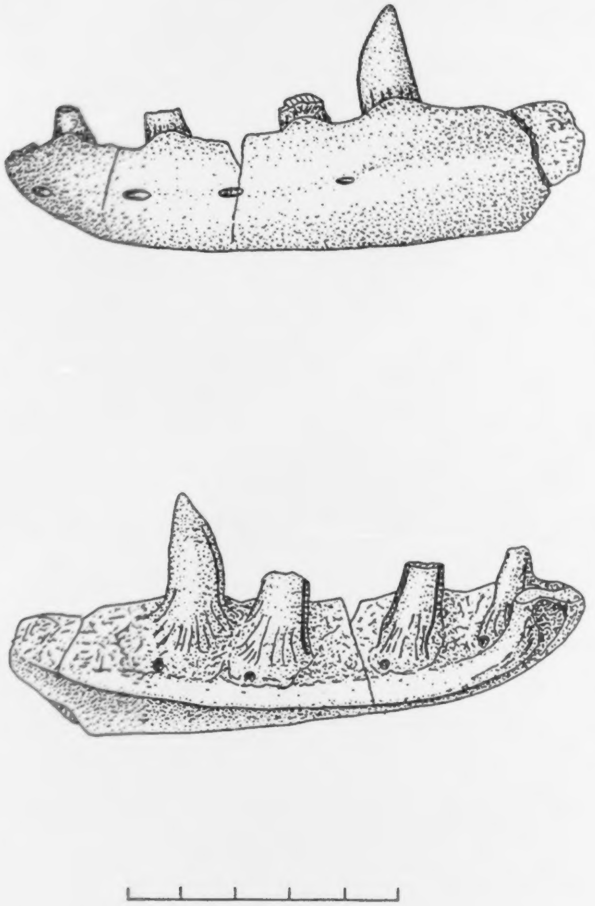
UALVP 29845 shows the first nine tooth positions of the jaw, including the first, third, fifth, seventh and eighth dentary teeth, and the spaces for the second, fourth, sixth, and ninth. This tooth-and-space pattern is obviously the result of an alternating pattern of tooth replacement. The first tooth on the jaw is mostly broken off, leaving only the basal part preserved. The eighth tooth is completely preserved, showing that the posterior teeth of this lizard are laterally compressed, having a trenchant crown without serrations. The remaining three teeth have the tips of the crowns broken off, but still show that the anterior teeth are more columnar than compressed, with pointed and recurved tips. These teeth are pleurodont, having the lower half of the tooth attached to the lateral parapet of the jaw. In agreement with the holotype maxillary (UCMP 54261, see Pregill et al. 1986, fig. 9; also see Plate 16, Figs.1-3 in this paper), the teeth in this dentary also show a taxonomically important character for this species: an incipient venom groove developed anteriorly on the tooth shaft (Plate 16, Fig. 5; Text-fig. 23), which is, however, less conspicuous and shallower than that in the Recent Heloderma. The fifth tooth also has a posterior groove, while the remainder do not. The tooth base is weakly infolded, and each tooth has a basal foramen developed medially.

The lateral surface of the dentary is smooth and is anteriorly strongly turned towards the symphysis in correspondence with the anterior curvature of the jaw. Four inferior alveolar foramina can be seen on the surface; and the fifth is not present, although the approximate location for this foramen is preserved on the jaw. These foramina are small in relation to the size of the jaw, and are slightly elongated and widely spaced from one another.

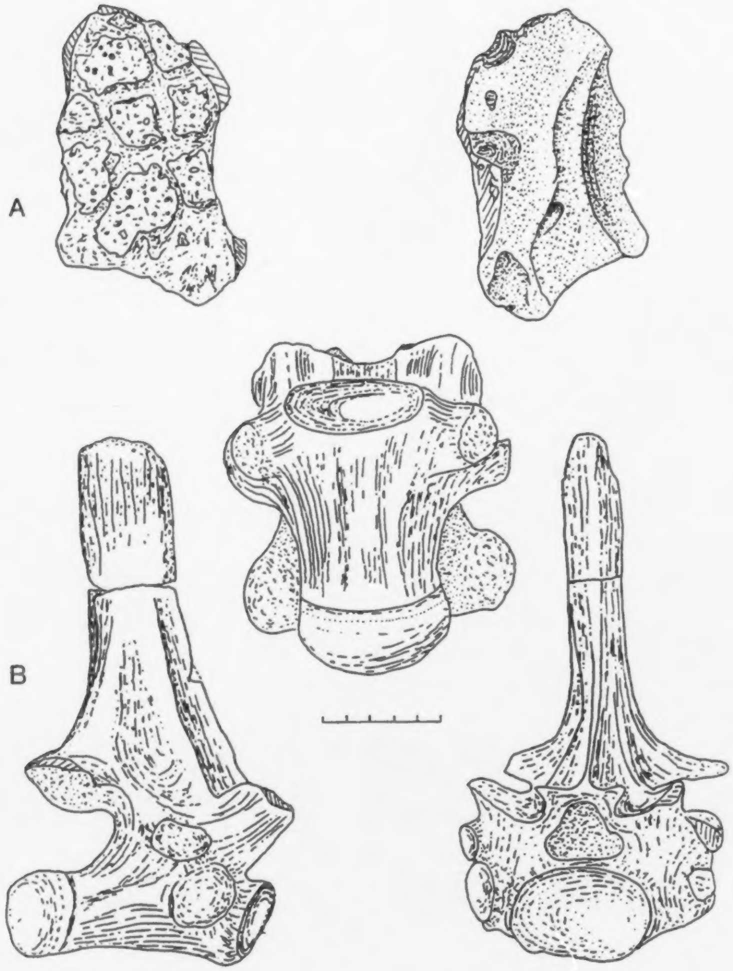
Another specimen, UALVP 29846, is the posterior part of a right dentary from the Wounded Knee locality. Although fragmentary, this specimen has one tooth and the spaces for three others preserved; more importantly, the specimen clearly shows that the ventral border of the intramandibular septum is largely free from the floor of the Meckelian canal (vs. Estes 1983a: 177), in contrast to Parasaniwa from the same horizon in which the septum is mostly fused to the canal floor.

Parietal.-UALVP 33385 is clearly referrable to Paraderma bogerti on the basis of its osteoscute pattern and is the first parietal known for this species (previous referral of YPM 1063 to this species [Estes 1964] was erroneous, see later discussion). Although incomplete, the specimen clearly shows a helodermatid synapomorphy: origin of the adductor muscles from the ventral surface of the parietal table (Pregill et al. 1986). The lateral border of the bone is comparatively straight (not strongly concave medially), indicating that the parietal must have been roughly trapezoidal in shape. The dorsal surface of the bone is covered with heavy osteoscutes that in pattern and surface texture are similar to those on the holotype maxillary (see Plate 16, Fig. 6). Another taxonomically and evolutionarily significant feature that this parietal shows is the presence of a small but clearly defined parietal foramen. In all Recent and the Tertiary fossil forms in which the parietal is known, the foramen is absent.

Vertebrae.-Nine disarticulated vertebrae (UALVP 33902-33910) from the KUA-1 locality are referrable to Paraderma bogerti on the basis of their general helodermatid morphology (see below). One of these (UALVP 33902) can be identified as a cervical vertebra, as it has a relatively low and wide neural spine compared to other vertebrae. Although not well-preserved, this cervical clearly shows no hypapophysis on the ventral surface of the centrum. Absence of the hypapophysis is considered as a synapomorphy for the Helodermatidae (Hoffstetter & Gasc 1967, 1969; Pregill et al. 1986; Estes et al. 1988). The remainder (UALVP 33903-33910) are well-preserved dorsal vertebrae. These show generalized varanoid features, such as a tapered centrum, a large and flanged condyle, and a precondylar constriction (Romer 1956). However, they are definitely of helodermatid type, as they have a slightly concave lateral border of the centrum (McDowell & Bogert 1954), and a neural spine that is narrow and tall (Pregill et al. 1986). In addition, the dorsal vertebrae of Paraderma bogerti differ from those of Palaeosaniwa canadensis and other varanids in having a less pronounced precondylar constriction, an anteriorly oriented condylar cup, and well-developed zygantra and zygasphenes (Text-fig. 24). Another important feature that these vertebrae show is that the diapophysis and parapophysis are separated; the condition in Recent Heloderma in this aspect has not been clearly described in previous publications to my knowledge, but Boulenger's (1891, fig. 5) figure seems show that the two processes in Heloderma are jointed to form a synapophysis (sensu Romer 1956) as in varanids.



Text-fig. 23. Helodermatidae, *Paraderma bogerti*, Scollard Formation, central Alberta; UALVP 29845, incomplete left dentary; (above) lateral view, (below) medial view. Scale = 5 mm.



Text-fig. 24. Helodermatidae, Paraderma bogerti, Scollard Formation, central Alberta; A - UALVP 33385, incomplete parietal, (left) dorsal and (right) ventral views. B - UALVP 33903, dorsal vertebra, (left) lateral, (middle) ventral and (right) anterior views. Scale = 5 mm.

Discussion: Estes (1964) founded *Paraderma bogerti* on several specimens from the Lance Formation, Wyoming. The holotype (UCMP 54261) is an almost complete left maxillary with thick osteoscutes fused to its lateral surface. As Estes (1964, 1983a) stressed, the obvious characters for this lizard are the *Heloderma*-like osteoscutes on maxillary and the strong medial curvature of the nasal process. In contrast to Estes' (1964: 133) statement that "internally the maxillary is identical with that of *Parasaniwa*," the holotype of *Paraderma bogerti* differs from the maxillary of *Parasaniwa* in having a strong fold of the supradental shelf, and having two posterior interior alveolar foramina that open close to the midpoint of the tooth row (pers. observ.).

The dentary morphology of *Paraderma bogerti* is poorly known, as the UCMP collections include only one poorly preserved specimen (UCMP 49939), which was neither numbered nor figured, but was described in Estes' (1964) review of the Lance lizards. The newly discovered specimens from the Scollard and Frenchman formations reveal, contrary to what Estes (1964, 1983a) presumed, that the teeth of this lizard are more high-crowned (shown on UALVP 29845) than those of *Parasaniwa*, and the intramandibular septum is free from the floor of the Meckelian canal (see UALVP 29846). The dentary of *Paraderma* is clearly distinguishable from that of *Parasaniwa* from the same horizon: in addition to its much larger size and massiveness, the dentary of *Paraderma* differs from the latter in having a more robust but less crescentic tooth-bearing border, much stronger symphysial process, and a free ventral border of the intramandibular septum, while the septum in *Parasaniwa* is mostly fused to the floor of the Meckelian canal (see Estes 1964).

Estes (1964) originally placed *Paraderma* together with *Parasaniwa* in his Parasaniwidae (=Necrosauridae Hoffstetter 1943) "on the basis of general tooth form [which was largely unknown then] and simple basal infolding of tooth bases" (Estes 1964: 134); he also noted the close resemblances to *Heloderma* in premaxillary morphology, snout shape, and osteoscute pattern. Accepting Hoffstetter's (1969) interpretation that Parasaniwidae and

Necrosauridae are closely related groups, and recognizing the incipient venom groove on the teeth of Paraderma, Estes (1983a) synonymized Parasaniwidae with Necrosauridae, and allocated Paraderma to the Helodermatidae, albeit with some uncertainty. That Paraderma is a helodermatid has been confirmed by a more recent revision of fossil helodermatids (Pregill et al. 1986).

The discovery of the parietal of Paraderma bogerti (UALVP 33385) is of special importance, as it provides solid evidence to clarify some taxonomic and evolutionary controversies of the Helodermatidae. Gilmore (1928: 158; pl. 27, fig. 3) placed an incomplete parietal (YPM 1063) from the Lance Formation that Marsh (1892: 450) had referred to Chamops segnis as "the upper part of the cranium" in his Megasaurus robustus (this name is a nomen dubium, although Estes 1983a listed it as the synonym of Palaeosaniwa canadensis). Estes (1964: 135; 1983a: 95, 177) referred YPM 1063 to Paraderma bogerti, but ambiguously commented that it "appears to belong to Palaeosaniwa as shown by the UCMP specimen of the latter." With the discovery of UALVP 33385, the characters of which demonstrate a taxonomic association with the holotype maxillary of Paraderma bogerti, the referral of YPM 1063 to P. bogerti is clearly in error. In fact, Gilmore's (1928, pl. 27, fig. 3) figure shows that YPM 1063 is certainly not helodermatid-like, since it has a strongly developed lateral flange; this flange indicates that the temporal musculature originated from the dorsolateral surface, while in helodermatids the temporal muscles are attached to the ventrolateral surface of the parietal table. Alternatively, an association of YPM 1063 with Palaeosaniwa, as Estes (1983a) suggested, is possible but quite uncertain, because skull elements of Palaeosaniwa are poorly known.

A Tertiary (upper Eocene or lower Oligocene) European helodermatid, Eurheloderma Hoffstetter 1957, is characterized by having a strongly constricted parietal (Hoffstetter 1957; Estes 1983a; Pregill et al. 1986). Yatkola (1976) regarded the constricted parietal as a derived condition, but without support from fossil evidence. Pregill et al. (1986: 190) pointed out that Yatkola's consideration "may be correct, but the parietal of Paraderma must be found to verify the polarity." Now, with the discovery of UALVP 33385, it can be shown that a wide and trapezoidal parietal is a primitive condition in the Helodermatidae. This statement is also supported by the discovery of another helodermatid parietal from the Oldman Formation (see description below).

Genus Labrodioctes n. gen.

Type and only known species: Labrodioctes montanensis n. sp..

Range: Upper Cretaceous, North America.

Diagnosis: As for the type and only known species.

Etymology: labros + dioktes (Gr., m.), meaning greedy hunter, in reference to the presumed predatory habit (feeding style) of this lizard.

Labrodioctes montanensis n. sp.

Plate 17, Figs. 1-5

Holotype: ANSP 18664, an incomplete left dentary having five teeth and spaces as well as broken bases of six others.

Type locality and horizon: Blackbird Ridge Site, Zeier Ranch, Golden Valley County, central Montana; Upper Cretaceous Judith River Formation (Judithian in age).

Referred specimen: RTMP 78.18.1, a fragmentary frontal with thick, fused osteoscutes; collected from White Rock Coulee, approximately 50 km north of Medicine Hat, southern Alberta.

Known distribution: Upper Cretaceous Judith River Formation, eastern Montana; Oldman Formation, southeastern Alberta.

Diagnosis: A Late Cretaceous very large helodermatid differing from Paraderma and other helodermatids by a combination of the following character states: size very large; dentary robust, with strong mandibular symphysis; dentary teeth, 12-13 in number, robust, not trenchant, but strongly recurved; venom groove absent.

Description: Collected by the CMNH and ANSP joint field party on July 11, 1991 from the above-described locality, the holotype (ANSP 18664) is a very large dentary (three times the size of the dentary of Paraderma). The specimen is anteriorly complete, but is broken posterolaterally at the seventh tooth position. ANSP 18664 has a robust, crescentic tooth-bearing border, which is more strongly dorsoventrally concave than in Paraderma but the curvature is not as strong as in Recent Heloderma. The anterior end of the bone strongly curves to the mandibular symphysis, and bears a prominent medioposterior projection (the symphysial process). The anterior half of the Meckelian canal is an extremely shallow sulcus that opens ventrally, curving to the strong mandibular symphysis. The posterior half of the canal is greatly deepened and triangular-shaped in medial view, widely open medially with the splenial missing. A well-developed intramandibular septum posteriorly separates the Meckelian canal from the lateral inferior alveolar canal. The septum is posteriorly broken, but the preserved part has a free ventral border, as in the Lance Paraderma (see above description). The posterior notch for the Meckelian cartilage is not preserved on this specimen.

As preserved, the dentary shows 11 tooth positions, including four complete teeth, four broken bases, and three vacant spaces as a result of tooth replacement. The dentary teeth are robust, having greatly thickened and fluted bases and pointed and strongly recurved crowns. Although the tooth crowns have weak anterior and posterior cutting edges (without serrations), they are not laterally compressed and are much less trenchant compared to those in Paraderma bogerti. The sixth tooth shows an incipient venom groove vertically along the anterior edge of the tooth, while the fifth and the seventh show a stronger groove on the medial surface of the teeth. These teeth are widely spaced from each other and are pleurodont, having the upper half of the tooth height projecting above the lateral parapet of the jaw. The last two tooth positions on the preserved part of dentary are associated ventrally with a sudden narrowing of the tooth-bearing border, where a large internal mental foramen (anterior inferior alveolar foramen) is located. This condition, plus the free ventral border of the intramandibular septum, indicates that probably only the posteriormost one or two teeth are missing from this specimen, yielding a total count of about 12-13 for the dentary tooth row.

The lateral surface of the dentary is mostly preserved, with the posterodorsal part broken. The surface is smooth, more flat than convex, and anteriorly turns medially to the mandibular symphysis. The four lateral mental foramina (lateral inferior alveolar foramina) that open to the surface are about equal in size and are evenly spaced from one another. These foramina are more or less almond-shaped, and are horizontally aligned along the middle depth of the jaw.

Discussion: The specimen described above (ANSP 18664) represents a Judithian helodermatid lizard, the obvious characters of which are its large size, robust and strongly recurved teeth that lack a well-defined venom groove. The size of this dentary suggests that the actual snout-vent length of this lizard was about 1-1.5 m, which is about three times the maximum length of Recent Heloderma (see Bogert & del Campo 1956; Pregill et al. 1986).

RTMP 78.18.1 (Plate 17, Figs. 3-5), a robust frontal from the Oldman Formatition of Alberta, is compatible in size with ANSP 18664, and is definitely helodermatid-like in having thick, polygonal osteoscutes, and the prefrontal and postfrontal incisions approaching each other above the orbits (see Plate 17, Fig. 5). The Oldman Formation in Alberta is geologically equivalent to the upper part of the Judith River Formation in Montana. Therefore, I believe that ANSP 18664 and RTMP 78.18.1 belong to the same species, unless another helodermatid-like varanoid of that age and of that size is involved (for which there is no evidence).

Morphologically, the dentary ANSP 18664 is Paraderma-like, as it shows a robust tooth-bearing border that is strongly curved dorsomedially at the anterior end, and it bears a strong mandibular symphysis. However, the Judithian dentary differs from that of the Lancian Paraderma bogerti not only by its large size, but in having strongly recurved, much less trenchant teeth that lack a definite venom groove. These differences, plus about 13 Myr. geologic gap (see Goodwin & Deino 1989), are great enough to separate it from Paraderma bogerti at the generic level. Therefore, I here recognize this Judithian form as a new genus and species. The lack of a definite venom groove on the dentary teeth slightly weakens its referral to the Helodermatidae, as the presence of this character state is regarded as one of the few unambiguous synapomorphies for the family (Bogert & del Campo 1956; Estes et al. 1988); however, several other characters strongly support its placement within the family. These include the following, which have been listed as helodermatid synapomorphies in Estes et al. (1988): (1) robust, broadened skull with short face, and rounded snout (McDowell & Bogert 1954; Romer 1956); (2) prefrontal and postfrontal approaching each other but not in contact above the orbits (Estes et al. 1988); and (3) thick polygonal osteoscutes fused to the skull elements (McDowell & Bogert 1954). Character state (1) is clearly indicated by the holotype dentary with strong symphysial curvature and fewer dentary teeth, while (2) and (3) are clearly shown on the referred frontal from the Oldman Formation. On the basis of these character states, Labrodioctes montanensis is placed in the family Helodermatidae, while the lack of a venom groove should be regarded as a primitive condition in the family (and it now is clear that the Lancian Paraderma has a weaker groove than Tertiary and Recent species in the family).

Mesozoic fossils of Helodermatidae are rare. Besides the Lancian Paraderma bogerti and Labrodioctes montanensis, a Campanian species, Gobiderma pulchra Borsuk-Bialynicka 1984, is known from the Central Asian Gobi Desert. Gobiderma pulchura was founded on several skulls and jaws from the Barun Goyot Formation (Khermeen Tsav II and Khulsan localities). The holotype (ZPAL MgR-III/64) is a nearly complete skull with a partial mandible from the Khermeen Tsav II locality. Although she noted the general similarities of this Gobi species to the Helodermatidae in general morphology of the skull, osteoscute pattern, and construction of the jaw, Borsuk-Bialynicka (1984: 39) placed Gobiderma in her "Necrosaurian grade, family uncertain." In a review of helodermatid evolution, Pregill et al. (1986) removed Gobiderma pulchrum from consideration as a helodermatid, stating that "the overall appearance of the skull recalls that of Xenosaurus" (Pregill et al. 1986: 195); they emphasized that Gobiderma is generalized in skull morphology compared to Heloderma (ibid.). From personal examination of the holotype and referred specimens of Gobiderma pulchrum, I here offer the following comments:

1) Gobiderma is definitely a varanoid, but not a xenosaurid, because it has plicidentine infoldings of the tooth bases (Borsuk-Bialynicka 1984; and pers. observ.).

2) Gobiderma shares several characters that are in combination unique to helodermatids: the jaw adductors have a ventral origin on parietal; the supradental shelf curves medially anteriorly; the osteoscutes are polygonal and fused to the skull elements; and the tooth number is reduced in correspondence with the shortening of the jaws.

3) However, Gobiderma differs from helodermatids in having a more pointed and longer snout, and in retaining a supratemporal opening.

From the above comparisons, Gobiderma appears to be more closely related to the Helodermatidae than to any other varanoids. I agree with Borsuk-Bialynicka (1984) who regarded Gobiderma as an Asian substitute of the American helodermatids, not ancestral to the Recent American helodermatids. North American Mesozoic helodermatids are mostly based on disarticulated jaws and skull elements while the teeth of Gobiderma are poorly known; therefore, the precise relationships and taxonomic status of Gobiderma will remain obscure before further study of better preserved materials for both North American and Asian forms.

No matter whether the Central Asian Gobiderma is or is not included in the family Helodermatidae, the North American Judithian Labrodioctes montanensis represents the earliest fossil record for the family; because the age of the Barun Goyot Formation in the Gobi Desert is probably younger than the Oldman Formation (Fox 1976; Jerzykiewicz & Russell 1991).

Helodermatidae, genus & species undetermined

Plate 17, Figs. 6-10

Specimens: RTMP 85.58.58, incomplete parietal; UALVP 33338, left tooth-bearing pterygoid.

Locality and horizon: RTMP 85.58.58 was collected from the Railway Grade locality, in Sec. 22, Tp. 20, R 12, W 4, and UALVP 33338 was from a site about 8 km upstream of Sandy Point; both Upper Cretaceous Oldman Formation (Judithian in age), southeastern Alberta.

Description: RTMP 85.58.58, from the Railway Grade locality, consists of the main part of a parietal table, with the posterior part and the supratemporal processes broken off. The parietal is broad and trapezoidal, lacking strong constriction of the middle part of the table. Besides its large size and different pattern of osteoscutes, this parietal differs from that of *Parasaniwa* in having the parietal fossa closely located to the large parietal foramen, and more importantly, in having a roof-like dorsolateral extension, rather than a ventrolateral flange, for the attachment of temporal musculature to the ventral surface of the parietal table (see Plate 17, Fig. 7). The latter feature indicates that the parietal is definitely helodermatid-like, not varanid-like. In ventral view, the specimen shows a small but deep parietal fossa, which is proportionally much smaller than that in *Paraderma bogerti* and is more closely located to the parietal foramen. The specimen is distinguishable from that of *Paraderma* by its large size, large parietal foramen, and thin and rounded osteoscutes. The parietal of *Paraderma* has a smaller parietal foramen but much thicker, polygonal osteoscutes. In spite of its large size, this parietal is not compatible in its robustness with the dentary and frontal of *Labrodioctes* (see above); therefore, it probably represents a helodermatid other than L. montanensis.

UALVP 33338 was collected by D. Brinkman from the bank of the South Saskatchewan River, about 8 km upstream from Sandy Point. The specimen is the anterior part of a toothed left pterygoid that can be tentatively referred to "Helodermatidae, genus & species undetermined" on its distinctly large size and Heloderma-like morphology. On this specimen, the basal plate is well-preserved, and the anteromedial (or palatine) process is nearly complete, with only the anterior tip broken. The process is short and broad, having an anteromedial depression for the pterygoid-palatine articulation. The anterolateral (or ectopterygoid) process is broken off from the basal plate; however, the specimen clearly shows a triangualr ventral depression between the diverging palatine and ectoperygoid processes; such a triangular depression indicates a short and wide skull, as it is developed in Heloderma, but not in Lanthanotus and Varanus in which the skull tends to be longer and more slender. The posterior (or quadrate) process, arising in front of the pterygoid-basisphenoid contact, is also missing. Posteriorly from the anterior part of the palatine process, the pterygoid bears a heavily-toothed area along the medial border of the basal plate. The teeth are fused to the plate in an apparantly random manner such that no particular pattern can be recognized.

Discussion: The general morphology of RTMP 85.58.58 indicates that the parietal is of helodermatid-type, as it shows a lateral flange on its ventral side for attachment of the temporal musculature, and osteoscutes are fused to the dorsal surface of the bone. However, the specimen is incompatible with RTMP 78.18.1 (see above) in robustness and sculpture pattern (see Plate 17, Figs. 6-7). Therefore, the parietal probably represents another helodermatid of Judithian age. The parietal of Labrodioctes montanensis is unknown, but is likely to have been much more robust and to have had thicker and more dense osteoscutes. In spite of its large size, RTMP 85.58.58 is more lightly built than the parietal of Paraderma bogerti, which is only half the size of the former.

As described above, the pterygoid UALVP 33338 is large and also likely to belong to a helodermatid. The size and robustness of this specimen are compatible with both Palaeosaniwa and Labrodioctes (in both genera, the pterygoid is unknown), and the possibility of its association with the former genus cannot be ruled out at present. Here I tentatively refer this specimen to "Helodermatidae, genus & species undetermined" on its helodermatid-like morphology, leaving its definite referral pending further study on more and better preserved materials when these become available.

Family Varanidae Gray 1827

Genus *Palaeosaniwa* Gilmore 1928

Type species: *Palaeosaniwa canadensis* Gilmore 1928.

Range: Upper Cretaceous, North America.

Diagnosis: As for the type and only known species.

Palaeosaniwa canadensis Gilmore 1928

Plate 18, Figs. 1-8; Text-fig. 25

1928 *Megasaurus robustus* Gilmore, pl. 27, figs. 1, 1a

Holotype: USNM 10864, a nearly complete dorsal vertebra collected by W. E. Cutler in 1913, from the Oldman Formation, near Steveville, central Alberta, Canada.

Referred specimens: RTMP 80.29.120, 80.20.37, incomplete maxillaries; UALVP 33337, RTMP 85.36.184, 89.36.101, 89.121.1, tooth-bearing dentaries; RTMP 73.23.1, 80.16.439, 81.22.55, 81.26.22, 82.14.42, 82.19.106, 82.31.30, 85.43.24, 85.65.13, 85.67.24 (total: 10), and UALVP 33339-33345 (total: 7), all isolated vertebrae; RTMP 73.7.1, 81.23.47, tibiae.

Locality and horizon: The specimens listed above were collected from various localities of the Oldman Formation in southeastern Alberta; details see description of the specimens below.

Known distribution: Upper Cretaceous Oldman Formation, southeastern Alberta; Judith River Formation, Montana (Sahni 1972, see discussion below). Post-Judithian occurrences of this species have been reported from the Lance Formation (Estes 1964), Hell Creek Formation (Estes et al. 1969), and Fort Union Formation (Sullivan 1982), but see discussion below.

Diagnosis (revised from Gilmore 1928; Estes 1983a): A Late Cretaceous large varanid from North America, closely resembling Saniwa Leidy 1870 in vertebral morphology, but differing from the latter and Recent Varanus in the following combination of character states: marginal teeth relatively short, broadly based; crowns constricted from tooth bases, slightly trenchant and recurved, having microserrations on both anterior and posterior cutting edges; vertebral neural spines robust, rod-like, with anterior crest.

Description: Among the specimens available for this study, several maxillaries and dentaries as well as other skull elements can be confidently referred to Palaeosaniwa canadensis on the basis of their large size (compatible with the size of the holotype vertebra) and varanoid tooth form. These specimens are important for providing, for the first time, information about characters other than vertebrae, on which the species was primarily based and from which the species has been long known, except for isolated teeth reported by Estes (1964) from the Lance Formation.

Maxillary.- Included in the collections for this study are two maxillaries that are the first known for Palaeosaniwa canadensis: RTMP 80.29.120, a left maxillary fragment from Sandy Point, South Saskatchewan River, about 20 km south of Empress, Alberta; and RTMP 80.20.37, a right maxillary fragment from the Dinosaur Provincial Park, Alberta.

The specimen RTMP 80.29.120 is especially important for it is the only known maxillary that bears a complete tooth of this species. The maxillary tooth is short, robust, and strongly recurved. The tooth base is greatly expanded and infolded, forming the so-called "honeycomb structure" (term used by Estes 1964). A small, round basal foramen is developed at the medial side of the tooth base. From the expanded tooth base, the tooth is greatly reduced in its thickness towards the apex, but has a medially swollen shaft. The tooth crown is more or less laterally compressed, strongly recurved, and has slightly trenchant anterior and posterior edges that bear microserrations. The specimen shows a large posterior interior alveolar foramen, which is close to the posterior end of the bone. This foramen indicates that the single tooth on the specimen is one of the posterior maxillary teeth, which may be slightly shorter and more robust than the teeth immediately adjacent anteriorly, which are in the middle part of the tooth row. Although fragmentary, RTMP 80.29.120 shows that the lateral surface of the facial process is ornamented with osteoscutes that are of the same pattern as on other skull elements (frontal and parietal) referred to the same species (see description below). The similar osteoscute pattern and the distinct large size of the specimens are the major reasons for putting these disarticulated bones into the same species.

RTMP 80.20.37 is the anterior fragment of a right maxillary, which bears a broken tooth and the base of another. The specimen shows that the maxillary has a strong base for the premaxillary process, and the facial process raises gently behind this base. The length of the premaxillary process is greater than that of Parasaniwa, but the process lacks the definite narial retraction seen in varanids such as Lanthanotus and Varanus. Medial and anterior to the facial process is the anterior interior alveolar foramen, which is almost as large as the posterior interior alveolar foramen (see RTMP 80.29.120 in which the latter foramen is preserved).

Dentary.- In this study, four dentary specimens (RTMP 89.36.101, 89.121.1, 85.36.184, and UALVP 33337) are referred to Palaeosaniwa canadensis. The large size and robustness of these dentaries are consistent with size and proportions of the holotype vertebra. The dentary teeth, having microserrations, are easily distinguishable from those of other North American Cretaceous varanoid taxa, such as Paraderma and Parasaniwa.

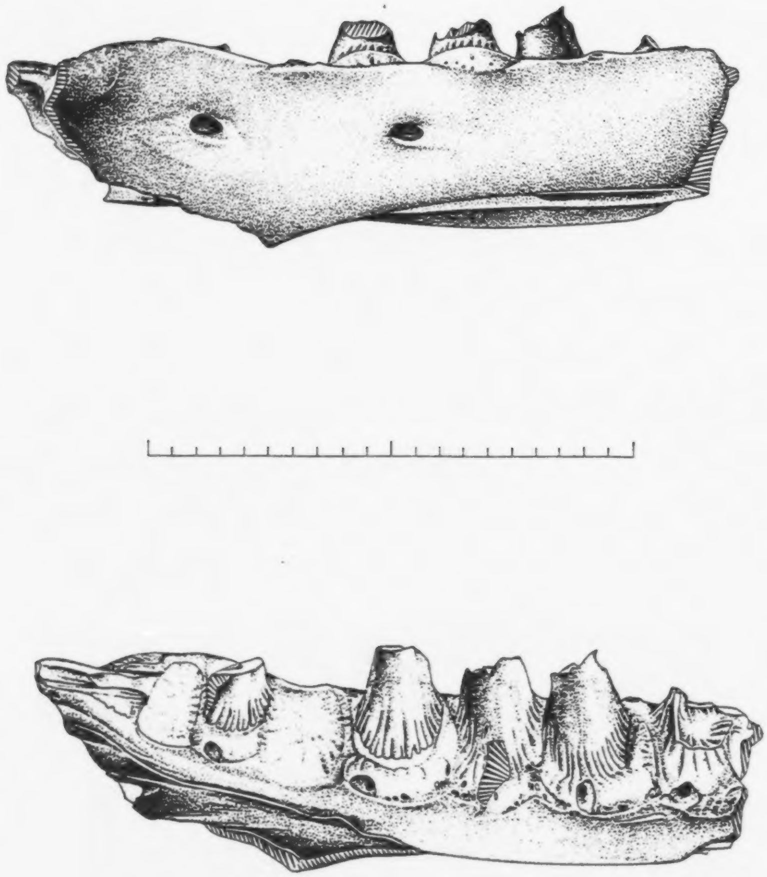
Among the four dentary specimens mentioned above, RTMP 89.121.1 is the best preserved in terms of showing both tooth form and the dentary structure of this lizard. This specimen has four broken teeth and the spaces for four others, representing the last eight tooth positions of the tooth row; the specimen is broken in front of the eighth tooth position from the back and along the ventrolateral border of the bone. Medially, RTMP 89.121.1 shows that the tooth-bearing border is much less crescentic than that of Parasaniwa. As commonly seen in other varanoids, the dental gutter on the medial side of the tooth row is entirely lost, and the subdental shelf is replaced by a ventrally growing ridge forming a medioventral border for the tooth row. Although the ventrolateral edge of the dentary is missing, the specimen clearly shows that the Meckelian canal is mostly open ventrally, with only the posterior portion below the last three teeth facing more medially than ventrally. A short but clearly defined intramandibular septum is developed below the last three and one-half tooth positions. It has a free ventral border that is clearly separated from the floor of the Meckelian canal and is developed as a prominent ridge-like structure, differing in those respects from the septum in Parasaniwa. The posterior edge of the septum is deeply notched for the Meckelian cartilage. Dorsal to the intramandibular septum is the coronoid facet, a deep groove running under the posterior tooth-bearing border for an interlocking articulation with the internal anterior process of the coronoid bone. The facet is extended anteriorly beyond the anterior end of the intramandibular septum by half of a tooth position, i.e., the facet is located below the last four tooth positions.

Four teeth are preserved on RTMP 89.121.1, but all have the the crown apex missing by breakage. The teeth are pleurodont, projecting half of their height above the lateral parapet of the jaw. As seen on the maxillary (RTMP 80.29.120), the tooth bases are greatly expanded and infolded with complex plicidentine. Each tooth has a basal foramen opening at medial side of a strong basal cement ring. The tooth shaft above the basal infoldings is laterally flattened, medially swollen, and anteriorly depressed, giving a roughly semicircular but anteriorly concave cross section (Text-fig. 25). Although the tooth apices are all broken off on this specimen, the parts that remain show that the crowns are laterally compressed and slightly recurved. Two teeth on the jaw (the six and the seventh from the back) clearly show microserrations on the anterior cutting edge of the teeth. The last three teeth are obviously smaller than those anterior to them. The tooth-bearing border of this specimen anteriorly curves dorsally, indicating that the anterior breakage on this specimen was close to the mandibular symphysis. Judging from the tooth size and the tooth-bearing border curvature, I estimate that the complete dentary tooth row of this lizard consisting of 11 or 12 positions.

The lateral surface of the RTMP 89.121.1 is smooth, with no fused osteoscutes, and bears inferior alveolar foramina that are widely spaced from each other; the last foramen is located close to the last dentary tooth, as in Varanus but not Parasaniwa. The lateral surface of this specimen is shallowly concave posterodorsally. The concavity in Heloderma houses the venomous gland, while in other varanoids it houses a large seromucous gland (Bogert & del Campo 1956; Kochva 1974; Saint Girons 1976). The depression of Palaeosaniwa is probably for a seromucous gland, as there are no venomous grooves developed on the dentary teeth of this lizard. In spite of having this lateral depression, the dentary is generally straight in dorsal view, lacking the distinct sigmoid curvature of helodermatids (McDowell & Bogert 1954).

Another specimen, RTMP 89.36.101, is an incomplete left dentary having six tooth positions (three broken teeth and the spaces for three others). The specimen shows that the jaw structure and the tooth form agree in every aspect with those of RTMP 89.121.1, except for its slightly larger size (indicating an older individual).

The final two specimens (UALVP 33337 and RTMP 85.36.184) are both fragmentary right dentaries with broken teeth preserved. UALVP 33337 represents the largest individual among the four dentaries used in this study; RTMP 85.36.184 clearly shows the basal infoldings and the cement around the tooth base. Both specimens show that the inner surface of the Meckelian canal is more deeply grooved than in the jaw of Paraderma.



Text-fig. 25. Varanidae, Palaeosaniwa canadensis, Oldman Formation, southeastern Alberta; RTMP 89.121.1, incomplete right dentary; (above) lateral view, (below) medial view. Scale = 20 mm.

Discussion: Gilmore (1928) founded the species name Palaeosaniwa canadensis on four isolated dorsal vertebrae (UA 112; USNM 10864, 11045; GSC 8510). The type specimen (USNM 10864) that he selected for the species was collected by W. E. Cutler in 1913, from a site near Steveville, Red Deer River, southern Alberta. Gilmore's naming of Palaeosaniwa canadensis is significant, as it documents the first North American Mesozoic varanoid and the first discovery of a terrestrial lizard from the Oldman Formation. On the other hand, his naming of this lizard taxon has created a long-term problem, because the species is founded solely on a vertebra; vertebrae of lizards are much less diagnostic than jaw materials, especially at generic and specific levels. This lizard has long been poorly understood, since Gilmore's original taxonomic treatment.

Gilmore (1928: 83) placed Palaeosaniwa canadensis in the family Varanidae on the basis of "the tapering form of the centrum with constricted condylar end" and the general similarity compared to the vertebrae of Saniwa Leidy 1870, a North American Eocene varanid. This familial assignment was questioned by McDowell and Bogert (1954: 53), who stated that Palaeosaniwa is "although definitely platynotan, not positively varanid." However, Estes (1964) added tooth form (trenchant crown with microserrations plus complex basal foldings) as new evidence to support the varanid affinity of Palaeosaniwa. Estes (1983a) cited the discovery of a Palaeosaniwa skull associated with vertebrae in UCMP collections; unfortunately, this important discovery has never been described or otherwise mentioned since. In this study, maxillary and dentary materials are described for the first time for this lizard. These materials are obviously compatible in size with the vertebrae on which the species is founded, and are morphologically clearly distinguishable from homologous parts of Parasaniwa, Paraderma, and Labrodioctes, the three other known North American varanoids of the same age. Therefore, these specimens are probably referrable to Palaeosaniwa.

Estes (1964) referred several vertebrae and isolated teeth from the Lance Formation to Palaeosaniwa canadensis. If the referral is correct, it will extend the geologic range of this lizard species from Judithian to Lancian. However, there are some uncertainties regarding the identification of the specimens: first, the isolated teeth without referrence to jaw structure are hard to demonstrate as different from those of Saniwa or other varanoids; and the "microserrations" that Estes (1964) figured seem too small and dense, compared to those on Oldman specimens described in this paper, to pertain to the same species. Second, the Lancian dorsal vertebrae (Estes 1964, fig. 66) show much weaker diapophyses and a more convex ventral surface of the centrum than those from the Oldman Formation (see Plate 18, Fig. 10). These suggest that the Lancian vertebrae may represent another varanoid, not Palaeosaniwa canadensis.

Estes et al. (1969) reported "Palaeosaniwa, cf. P. canadensis" from the Hell Creek Formation of eastern Montana. The specimen for this identification was a single large vertebra (MCZ 3665) that was neither figured nor described in detail. The specimen was characterized as having "convex lateral borders of the centrum", suggesting a varanoid affinity; however, lack of information on the morphologies of the condylar cup, precondylar constriction, and neural spine makes the referral of this specimen to Palaeosaniwa canadensis uncertain.

Sullivan (1982: 1007) recorded "cf. Palaeosaniwa canadensis" from a fragmentary dentary (AMNH 15957) from the Fort Union Formation, Wyoming, and stated that "the labyrinthine morphology of the tooth bases is the major criterion for referring this specimen to Palaeosaniwa canadensis. Assuming the assignment is correct, Palaeosaniwa's range is extended from the Late Cretaceous (Gilmore, 1928; Estes, 1964) to the middle Paleocene (Torrejonian)." Actually, having basal dentine infolding is broadly synapomorphic for Varanoidea (Estes et al. 1988), not uniquely for Palaeosaniwa canadensis; and thus, both Sullivan's identification and his claim of a Paleocene record of Palaeosaniwa are unconvincing. Estes (1983a: 184) made the following comments on this matter: "The fragmentary nature of the specimen, as well as the fact that Sullivan gave no measurements or figure, makes any definite statement impossible." In fact, Sullivan (1982) reported a Saniwa vertebra from the same locality. From his description, however, I see no reason for assigning the vertebra to "cf. Saniwa sp." but the dentary fragment to "cf. Palaeosaniwa canadensis." A more likely possibility is that the two specimens pertain to the same species.

EVOLUTIONARY HISTORY AND PALEOBIOGEOGRAPHY OF THE FAMILY TEIIDAE

Among various modern lizard families, the Teiidae (s. str.) are deserving of special attention for their relatively complete fossil record and complex evolutionary history. The Cretaceous fossil record of the Teiidae shows that the family had a wide geographical distribution in contrast to its concentration in Central and South America today. Here, I discuss the evolutionary history and the possible biogeographic origin of the family on the basis of our current knowledge of the group from the fossil record.

I. Taxonomic History and Phylogenetic Relationships

The taxonomic structure of the family Teiidae (s. lat.) is based on Boulenger's (1884, 1885) work, in which he assigned some 40 genera from several different families (see Boulenger 1885 for citations) to the Teiidae. In volume II of his "Catalogue of the Lizards in the British Museum (Natural History)," Boulenger (1885) subdivided his Teiidae into four groups, later cited by various authors as group I-IV (e.g., MacLean 1974; Presch 1974a), or less precisely as group A-B (e.g., Vanzolini & Valencia 1965) or groups I-II (e.g., Estes et al. 1988).

Sinitsin (1928) recognized two different skull types in teiids: type A, or platyrrhine, and type B, or catarrhine (terms borrowed by Sinitsin from anthropoid classification), on the basis of relative positions of the nasal cavity and Jacobson's organ. His type A corresponds to Boulenger's groups II-IV together, and his type B is correlative with Boulenger's group I. Sinitsin's (1928) work marks the first approach to the two group (later subfamilies, then families) subdivision of the family Teiidae (s. lat.); and this classification has been further developed by Ruibal (1952), Presch (1970, 1973, 1974a, and 1983), MacLean (1974), and

Estes (1983a). Subsequently, Boulenger's group I (= Sinitsin's B) became informally known as "macroteiids" and his group II-IV (= Sinitsin's A) as "microteiids." [1]

MacLean (1974) and Presch (1974a) separately recognized macroteiids and microteiids as different subfamilies: Teiinae (Presch 1974a) and Gymnophthalminae (MacLean 1974), respectively. More recently, Estes (1983a) and Presch (1983) independently ranked the two groups as families (Teiidae and Gymnophthalmidae). These studies have set a commonly accepted framework for the classification of Teiidae.

Although both Estes (1983a) and Presch (1983) were in agreement in separating macroteiids from microteiids at the familial level, they had different views on the relationships of the two families: Estes (1983a: 97) considered that "Gymnophthalmids may be most closely related to teiids," while Presch (1983: 189) suggested that teiids are "closely aligned with the Iguanomorpha while the gymnophthalmids are related to the lacertids." In fact, the sister group relationship of Teiidae with Gymnophthalmidae has long been recognized, as they were put in the same family Teiidae (s. lat.) in Boulenger's (1884, 1885) work. In the most recent phylogenetic analysis of the modern lizard families, Estes et al. (1988) listed 14 synapomorphies to unite Teiidae and Gymnophthalmidae in a higher taxon, Teiioidea Estes et al. 1988, which is closely related to Lacertidae (see Estes et al. 1988; but also see Schwenk 1988). Separate analysis by Presch (1988) scored the same phylogenetic relationships between these groups, although he used a slightly different set of characters.

On the basis of brain morphology, Northcutt (1978) proposed an untenable hypothesis: he named a new taxon Dracomorpha, in which the Teiidae and the Varanidae are sister groups, and the two together are more closely related to Iguania than to any of the other groups. This hypothesis is undefendable, because the relationships of the Varanidae within the Anguimorpha, and the Teiidae within the Scincomorpha are well-corroborated with various sources of evidence; whereas Northcutt's "Dracomorpha hypothesis" violates the monophyly of all the three well-established infraorders. Therefore, the characters on which this hypothesis is based must be re-evaluated.

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[1] The term "microteiids" was first used by Ruibal (1952), while "macroteiids" must occur in the literature later sometime between 1952 and 1965; because the latter term was unmentioned in Ruibal (1952), but Vanzolini & Valencia (1965: 19) stated that: Macroteiids as "a formally undefined but very convenient term which has crept into the literature, as applied to group A of Boulenger's key to the family in his Catalogue (1885)."

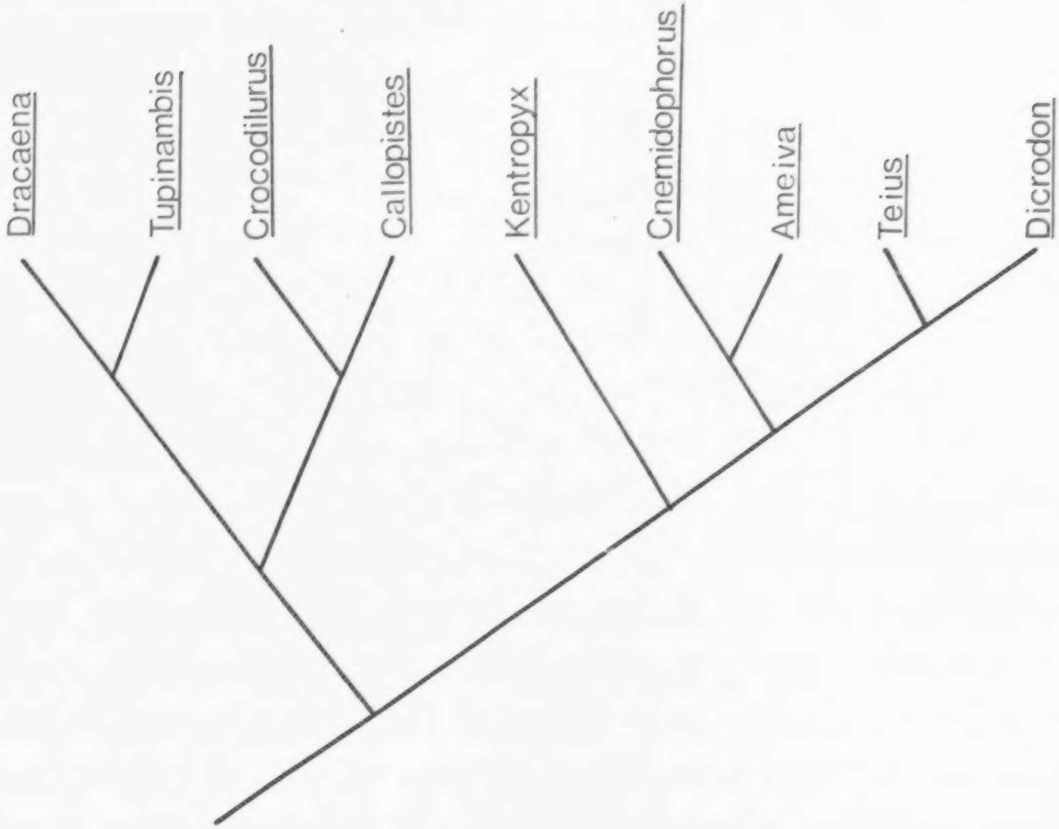
The monophyly of the Teiidae (s. str.) is supported by evidence from both osteology and myology (Romer 1956; MacLean 1974; Presch 1974a, 1988; Rieppel 1980; Estes 1983a; Estes et al. 1988), and from inner ear structures (R. S. Schmidt 1964). Two studies (Gorman 1970; Presch 1974a) comprise the major contribution to the reconstruction of the intrageneric relationships within this group.

On the basis of karyotype analysis, Gorman (1970) recognized three major groups in Teiidae (s. lat.). His giant or Dracaena group, consisting of four genera, is characterized by having "2n=34-38 chromosomes including five or six pairs of large metacentric macrochromosomes and a series of much smaller mirochromosomes" (Gorman 1970: 230); and his Ameiva group, including five genera, differs from the former in having "2n=46-56 chromosomes, general absence of a distinct break between macro- and microchromosomes, and a majority of large chromosomes acrocentric" (ibid.). The two groups were ranked early as tribes (Presch 1970, 1974a; Estes 1983a), but lately as subfamilies (Presch 1983; Estes et al. 1988); nevertheless, different ranking has no influence on their phylogenetic relationships. Gorman's third group, the microteiids, belongs to another family (Gymnophthalmidae) in current classifications.

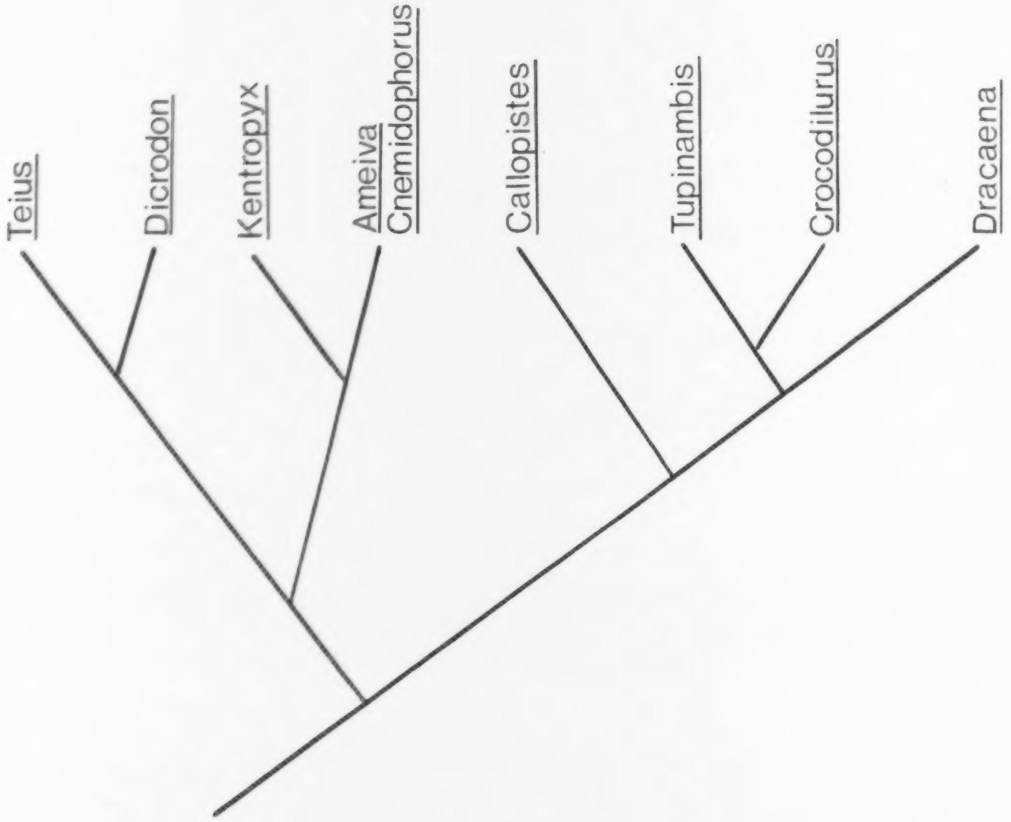
According to Gorman's (1970: 233) analysis, the Dracaena group (= Tupinambinae) shares a generalized karyotype that is "characterized by satellites on # 2 (fig. 2, a-e)," and this karyotype is apparently a primitive character state within the family Teiidae. The complex karyotypes of the Ameiva group (= Teiinae) are more variable than that of the giant group, and may have derived from the latter primitive state by centric fissions of the metacentric macrochromosomes (Gorman 1970: 230). Gorman's reconstruction of the intrageneric relationships in the Teiidae is modified and shown in Text-fig. 26.

Data other than osteology and myology are often so scattered that they are unavailable for phylogenetic reconstructions of lizards. Gorman's chromosome analysis provided a significant new approach to the phylogeny of the Teiidae. However, his interpretations of these data may need to be justified from the scope of today's methodology of phylogenetic analysis, because his reconstruction requires several unnecessary character reversals. Gorman (1970: 236-237, fig. 6) interpreted the primitive condition for Teiidae to be "a karyotype with six pairs of metacentric macrochromosomes and 12 pairs of microchromosomes" because this karyotype is found in many lizard families. From this "6 + 12" karyotype the two diverging lineages were derived, Dracaena group and Ameiva group. The evolution of the former group apparently has taken place by adding or losing microchromosomes accompanied by minor changes of metacentric macrochromosomes, while the latter group is characterized by drastic change of the macrochromosomes with relatively stable microchromosomes.

For the Dracaena group (= Tupinambinae), Gorman's reconstruction indicates that Callopistes, Tupinambis and Dracaena share a "6 + 13" karyotype, which is derived from the primitive "6 + 12" karyotype by centric fission of the sixth pair of macrochromosomes and by adding an extra microchromosome. The problem is that the branching of Callopistes requires a macrochromosome reversal (pair # 6) to the primitive condition, and the branching of Tupinambis requires another reversal of the microchromosomes. Evidently, a more parsimonious interpretation will logically avoid these reversals. It seems to me that the phylogenetic reconstruction of the Dracaena group can be modified as shown in Text-fig. 26.


Dracaena
Tupinambis
Crocodilurus
Callopistes
Kentropyx
Cnemidophorus
Ameiva
Teius
Dicrodon

Text-fig. 26. Phylogenetic relationships of the Teiidae, according to Gorman (1970) on chromosome analysis.


Teius
Dicrodon
Kentropyx
Ameiva
Cnemidophorus
Callopistes
Tupinambis
Crocodilurus
Dracaena

Text-fig. 27. Phylogenetic relationships of the Teiidae, according to Presch (1974) on osteology.

As for the Ameiva group (= Teiinae), Gorman's (1970, fig. 8) reconstruction can be modified as in Text-fig. 26. On Gorman's karyotype data, Kentropyx + Cnemidophorus + Ameiva form one monophyletic subgroup of the Teiinae, because they share a "13 + 12" karyotype, which may have derived from a "6 + 12" condition by centric fission of the six pairs of macrochromosomes and adding one macrochromosome. Another subgroup, consisting of Teius + Dicrodon, is united by centric fission of the inverted macrochromosomes. Within the latter subgroup, some macrochromosome reversals are obviously unavoidable for the branching of Teius.

Presch (1974a) presented another phylogenetic analysis of the Teiidae. By using the average linkage method, he placed the nine modern teiid genera into two groups (group A + group B) on 21 osteological characters. As shown in Text-fig. 27, his subdivision of the Teiidae into two groups generally corresponds to that of Gorman on chromosome analysis, but has a different arrangement of the four genera in his group B (= Gorman's "giant" group), in which Callopistes is the sister group of Tupinambis + Crocodilurus and Dracaena. The major difference between the two reconstruction schemes is in their different interpretations of evolutionary polarity, that is, on which is more primitive than the other among the two groups. Presch (1974a, table 4) considered the Tupinambinae (his group B) to be more advanced than the Teiinae (his group A), because the former group shares a greater number of derived character states (but see later discussion); while Gorman (1970) believed that the advanced karyotypes in the Teiinae (his Ameiva group) can be derived from the more generalized "6 + 12" karyotype of the Tupinambinae (his "giant" group) through centric fissions of the metacentric macrochromosomes. On this disagreement, I here offer the following comments:

1) Gorman's interpretation of the teiid evolutionary trend seems to be more plausible, since the more complex and more variable karyotypes of the Teiinae are logically more advanced than the much more generalized "6 + 12" karyotype of the Tupinambinae.

However, the problem is that this interpretation is based on the assumption of a "6 + 12" karyotype to be primitive condition for the Teiidae, while lacking solid evidence to support this assumption. From previous authors, the primitive "6 + 12" karyotype is found in some iguanid lizards (Gorman et al. 1967), in some anguids (Bury et al. 1969) and in gerrhosaurine cordylids (Matthey 1949; Gorman 1970), but not in the sister group of the Teiidae (Gymnophthalmidae and Lacertidae) according to Gorman (1970). If the "6 + 12" karyotype in gerrhosaurines is homologous to that of the presumed ancestral condition in Teiidae, this karyotype is certainly not a synapomorphic character for the Teiidae, but a symplesimorphic condition for a higher taxon that includes Teiidae, Gymnophthalmidae, Lacertidae, and some other families.

2) Presch's (1974a) analysis certainly has resulted in the most plausible phylogenetic reconstruction of intrageneric relationships of the Teiidae based on osteology. However, his interpretation of the Tupinambinae as more derived than the Teiinae is questionable because it is largely based on poorly polarized character states from the postcranum. At least two characters (coded as f/F, g/G) are apparently misinterpreted in his analysis: The rod-like clavicle and the clavicle hook are coded as derived conditions, but likely are primitive since they are shared with the closest sister group Gymnophthalmidae (see Presch 1980; Estes 1983a). Some of the characters Presch used are poorly quantified (e.g., long vs. short; much vs. small). The most reliable cranial osteologic data that Presch presented show that the Teiinae share a greater number of derived character states than the Tupinambinae (see Presch 1974a, table 4, characters coded as a/A, b/B). The other two characters (coded as c/C, d/D) are problematic: only Tupinambis is known as having no dorsal process of the squamosal (Reese 1923), while this same character is miscoded for Callopistes and Dracaena because the latter genera do have a dorsal process, although small (Estes 1983a; and pers. observ.). Estes et al. (1988: 150) pointed out that this character is variable within Dracaena and Tupinambis; accordingly, loss of the dorsal process of the squamosal may be significant for some species

of these genera, but is not likely to be a derived condition for the Tupinambinae at subfamilial level. Another character (d/D) is relatively unreliable because the development of pterygoid teeth is frequently variable in various lizard species (e.g., Estes et al. 1988).

3) Besides the karyotype data that Gorman (1970) has presented, other data suggests that the Tupinambinae are generally more primitive than the Teiinae, although both subgroups include highly specialized forms. Osteologically, Tupinambinae share at least the following primitive character states with Gymnophthalmidae (the sister group of Teiidae), which have been lost in the Teiinae: a) separation of postorbital from postfrontal (Reese 1923; Presch 1970, 1980; Rieppel 1980); b) functional frontoparietal joint, which is lacking in Teiinae (MacLean 1974: 185), but a "tab-joint" in two specialized gymnophthalmids (Presch 1980); and, c) presence of clavicle hook (Presch 1974a, 1980; Estes 1983a). Myologically, Callopistes (the basal taxon of the Tupinambinae) shares with the Gymnophthalmidae but not the Teiinae, a similar hyoglossus musculature having the same insertion: "Callopistes and the Gymnophthalminae are primitive in this regard" (MacLean 1974: 193). In addition, a comparison of the quadrate aponeurosis muscle also suggests that the tupinambine condition is more primitive than that of Teiinae (Rieppel 1980: 10).

4) Fossil evidence indicates that the splitting of Teiinae from the Tupinambinae may have taken place no later than mid-Campanian, as the North American Judithian teiids (Oldman Formation) include fossil genera of both groups: Socognathus shows Tupinambinae affinity (Gao & Fox 1991), as it bears character states such as heterodonty and suppression of tooth replacement in old adults; and Leptochamops is close to Teiinae, as Estes (1964) recognized.

From the above discussion, two authors (Gorman 1970; Presch 1974a) have come to similar results in subdividing the family Teiidae, but have different interpretations on which subgroup is the more primitive. There are some suggestions that the Tupinambinae are generally more primitive than the Teiinae, but a more plausible phylogenetic reconstruction of this lizard group needs to be made on a more extensive survey of characters and on a careful evaluation of various characters presented by previous authors. However, phylogenetic analysis of the Teiidae is beyond the scope of this study.

II. Recent Teiid Distribution and Three Hypotheses of Biogeographic Origin

Recent teiids are essentially Central and South American in distribution, with the exception of Cnemidophorus occurring in North America. Their distribution ranges from the northern part of the United States, through Mexico and Central America including the West Indies, to the southern part of South America. This distribution pattern, coupled with the greater diversity of the group in South America, has served as the main basis for herpetologists arguing for South American endemism of the group. However, the fossil evidence indicates that teiids were widely distributed in North America and Central Asia during Cretaceous time, while South America has a very poor fossil record of this group. This inconsistency between the distribution of Recent and fossil teiids, like that of marsupials, makes determination of the biogeographic origin of the family difficult. Each of the relevant areas (South America, Asia, and North America) can be put forward as the centre of origin of the Teiidae.

The first and once popular South American origin hypothesis is best summarized as "the evolution of teiids took place primarily in South America, where they are most diverse and widely distributed today" (Baez & Gasparini 1979: 41). The hypothesis explains the occurrence of teiids in Central and North America today as a result of invasion of the group from the south across the Panamanian Land Bridge sometime in the Tertiary. The origin of the family is explained by the separation of South America from Africa, producing teiids in the former and lacertids in the latter (see Estes 1970; Cracraft 1973a). This hypothesis is unconvincing, for the following reasons: 1) the hypothesis is unable to explain the early age and primitiveness of the Cretaceous fossil record of teiids in North America and Central Asia (see discussion below); 2) the wide distribution and greater diversity of the Recent teiids in South America today only reflects a recent successful adaptive radiation, which may largely be related to ecological factors and is not necessarily an indication of endemism or place of origin; 3) furthermore, the present study indicates that the family had an early diversification in North America in the Late Cretaceous, and shows that the group was more taxonomically diverse in North America than it is today in South America.

The second hypothesis, proposed by Presch (1983), can be summarized as: "the Teiidae originated in the northern landmasses and extended into North America from Asia and south into South America" (Presch 1983: 194). This hypothesis, gaining support from Borsuk-Bialynicka (1991: 10) "on the basis of their differentiation evidenced in the Late Cretaceous of Mongolia," provides a better approach than the South America origin hypothesis in terms of the dispersal direction; however, our current understanding of the fossil record of Teiidae is incongruent with this hypothesis. The definite Cretaceous fossil teiids from Asia are polyglyphanodontines and some possible tupinambines from the Gobi Desert. These Gobi teiids are geologically much younger than the North American Comanchean record (Winkler et al. 1990, and see further discussion below), and are morphologically too derived, in terms of tooth form or cusp pattern (strongly heterodont or polycuspid), to be or close to the ancestral stock of Teiidae. They are not ancestral to, but are instead "apparently derived from North American forms" (Estes & Baez 1985: 146). Other teiids or teiid-like lizards reported from Central Asia (Nessov 1985, 1988) are taxonomically unconfirmed and their geological ages are still questionable (see later discussion).

The third hypothesis (Presch 1970, 1974a; Estes 1983b) proposes a North American origin of the family Teiidae probably sometime during the Early Cretaceous or even Late Jurassic; then after a short diversification, teiids would have dispersed south to Central and South America, and northwest to Asia (see later discussion). Estes (1964, 1969a, 1970, 1983a-b) stressed the possible relationships of several North American Lancian teiids with Recent forms from South America, including: Chamops with Callopistes, Leptochamops and Meniscognathus together with the Recent Kentropyx-Cnemidophorus-Ameiva group, and Peneteius with Teius and Dicrodon. More importantly, recently recovered fossil teiids from the Comanchean (Early Cretaceous) of Texas are geologically much older and morphologically more primitive than any fossil teiids known from South America and Asia, in favor of the North American origin hypothesis. On the basis of current understanding of the fossil record of teiids, it seems appropriate to modify the North American origin hypothesis as in the following section.

III. Evolutionary History and Paleobiogeography

As mentioned before, Cretaceous fossil teiids are known from both North America and Central Asia, and probably also from South America (if Pristiguana Estes & Price 1973 from Brazil is indeed a teiid, and not an iguanid). The North American fossil record offers the most important information about the origin and evolution of the family Teiidae, in terms of both geological range and species abundance. The earliest known teiid fossils are those from the Lower Cretaceous of central Texas (Comanchean). Murry et al. (1989) reported the discovery of a microvertebrate fauna from the Comanchean Trinity Group (Twin Mountains, Glen Rose, and Paluxy formations), which includes several lizards of late Early Cretaceous age. The detailed description of this fauna was published by Winkler et al. (1990), who correctly referred three jaws (SMU 72282-72283, 72301) to the Teiidae. These jaws show synapomorphic character states of the Teiidae, such as extensive basal deposit of cementum (see Winkler et al. 1990, fig. 6c), a hypertrophied splenial as indicated by the widely open Meckelian canal, and subcircular replacement pits developed posteromedially at the tooth bases (see Estes et al. [1988] for citations). In addition, other character states, such as a well-developed subdental shelf and sulcus dentalis, are also indicative of the family Teiidae. According to Winkler et al. (1990: 112), these "Comanchean lizards are similar to modern teiids in the morphology of the Meckelian groove, splenial, and mode of tooth replacement, but are primitive in their tooth morphology." Most Recent and Lancian Cretaceous teiids have bicuspid or tricuspid teeth, while the Comanchean teiids are clearly conical in tooth form. Judithian teiids are predominantly unicuspid, although some tricuspid forms are known. This general change of cusp pattern corresponding to the geologic time range strongly suggests that the conical tooth form is primitive for the family Teiidae (Gao & Fox 1991). According to Winkler et al. (1990), the Comanchean fauna also includes some lizards that are similar to the Late Jurassic paramacellodids, indicating a transitional fauna between that of the Late Jurassic and Late Cretaceous. Other North American Cretaceous teiids are of Aquilan (Milk River), Judithian (Oldman, Judith River), and Lancian (Lance, Hell Creek, Scollard, and Frenchman) age.

Central Asia is another place of importance for the teiid fossil record. Nessov (1985, 1988) questionably referred Buckantaus crassidens from the Taikarshin beds (now the Bisszkty Formation, L. Nessov pers. comm., 1991), Kizylkum Desert of Uzbekistan to the Teiidae and identified other materials from the Jalovatsh Formation, Kansay, as "small teiid-like lizards." The geologic ages of these beds are claimed to be Coniacian-Santonian, but both the taxonomic assignment and the geologic ages of these lizards are still uncertain, since the specimens are not well preserved and the ages are determined by using shark teeth and brackish water molluscs that are biostratigraphically unreliable in most cases. The taxonomic revision of these lizards is being undertaken by Nessov and the present author.

The Central Asian Gobi Desert has yielded one of the largest collections of Cretaceous lizards known. Since the 1920s, more than 500 specimens of several families have been collected from the Djadochta and Barun Goyot (including Khermeen Tsav) formations. The fauna includes several genera of the Polyglyphanodontinae (sensu Estes 1983a):

Macrocephalosaurus Gilmore 1943, Adamisaurus Sulimski 1972, Darchansaurus Sulimski 1975, Cherminsaurus Sulimski 1975, and Erdenetesaurus Sulimski 1975. Although lack of consensus about the suprageneric classification of these lizards exists (see Sulimski 1975, 1978; Estes 1983a), it is clear that these forms are highly derived in terms of tooth morphology compared to the Comanchean teiids of North America. In addition to these polyglyphanodontines, Alifanov (1988) added two new genera, Mongolochamops and Piramicephalosaurus, that seem to have affinities with the Tupinambinae. Recent reviews of the the fossil vertebrates from the Gobi suggest that the Djadochta Formation is probably mid-Campanian in age (Fox 1978; Lillegraven & McKenna 1986; Jerzykiewicz & Russell 1991). Therefore, the Gobi teiids are probably significant for understanding the early adaptive radiation of teiids, but provide little information for determining the place of origin for the family. The highly derived teiids from the Gobi Desert indicate that a group of polyglyphanodontines was once successfully adapted to an arid or semi-arid desert environment that is different from the North American humid subtropical or warm temperate environment contemporary with it.

The South American continent offers little information about the evolutionary history of the Teiidae, because of its poor fossil record. The earliest known fossil teiids in South America are from the late Paleocene of Brazil: Estes (1970) reported "teiid remains" from the Paleocene Itaborai deposits of Brazil, that consist of specimens that are still uncatalogued and unidentified at generic and specific levels. Estes (1983a:) listed these specimens as "Teiidae incertae sedis" and commented that "both teiine and tupinambine groups are represented and at least two Holocene genera may be present" (Estes 1983a: 97). Another possible teiid record in Brazil is from the Upper Cretaceous Bauru group (now divided into three formations). Estes & Price (1973) reported Pristiguana, a supposed early iguanid, from the group, but both their original description and later review (Borsuk-Bialynicka & Moody 1984) indicate that it could well be a Leptochamops-like teiid, rather than an iguanid; moreover, the Late Cretaceous age of this formation is highly questionable, and could be Paleocene (Van Valen

1988).

The fossil record of the Teiidae outlined above suggests that the family may have originated sometime during the Early Cretaceous or Late Jurassic, somewhere in North America. The ancestral stock of the family is probably closely related to the Old World lacertoid group. The close relationship of the New World Teiidae with the Old World Lacertidae has long been recognized, and is supported by evidence from osteology, ecology, tongue musculature, and cochlear nerve structures (Camp 1923; Romer 1956; R. S. Schmidt 1964; Underwood 1971; Rieppel 1980; Estes et al. 1988; Presch 1988; Schwenk 1988).

The splitting of the Teiidae from its ancestral stock is probably associated with a vicariant event (Estes 1983b), which caused a small population of lacertoids to be separated geographically from its parental stock. During the Late Jurassic - Early Cretaceous, the North American block started moving westward away from the Eurasian block as a consequence of the re-opening of the North Atlantic Ocean (see, e.g., Cracraft 1973b; Irving 1977; Irving & Irving 1982). This event may have caused a small population of lacertoid lizards to be isolated from its Eurasian parental group. Then in eastern North America, this population could have undergone rapid diversification under new selection pressures in a subtropical or warm temperate environment with abundant food.

After a short radiation in North America, this new group of lizards may have dispersed south to Central and South America, and west to Asia. The invasion of teiids to Central and South America probably happened sometime during the Late Cretaceous (Estes & Baez 1985). According to Rage (1981, 1988) and Bonaparte (1984a-b), a land route was already available for the interchange between North and South America; however, the current known fossil record of the Teiidae indicates that the family had two major radiations at middle Campanian and late Maestrichtian in North America, while the earliest known record from South America is latest Cretaceous or early Paleocene (see discussion above). These fossil evidence favors a Maestrichtian southward dispersal of the Teiidae. This interpretation about the timing of the invasion is well corroborated by the North American fossil record, as the Lancian "lizard fauna of North America includes a number of teiid lizards that show clearly relationship to teiid groups limited today to South America" (Estes & Baez 1985: 145), while Judithian and Aquilan teiids are far less clearly related to modern teiids of South America. Although the Maestrichitian Pristiguana maight be a Late Cretaceous teiid in South America, the family was not well established until the Paleocene. The early teiids may have arrived in South America across a "Panamanian Land Bridge" (Savage 1966, 1982; Presch 1974a), which was formed as early as Campanian (Bonaparte 1984a), or may have utilized volcanic arc islands as "stepping stones" (Dengo 1968, 1973; Lillegraven et al. 1979; Coney 1982). Hadrosaurs and some other vertebrates may have used the same route to invade South America (Rage 1978, 1981, 1986, 1988; Bonaparte 1984a-b; Estes & Baez 1985). The dispersal of teiids to Asia, from the current fossil evidence, was probably sometime during the early Late Cretaceous or even earlier, across the Bering Land Bridge, which may have linked Asia with North America since Cenomanian time (see, e.g., Colbert 1973; Parrish et al. 1987; Moody 1990; Jerzykiewicz & Russell 1991) or even earlier, as suggested by the occurrence of congeneric triconodont mammals in both North America and Asia (Jenkins & Schaff 1988). Some dinosaurs, turtles, and some mammals may have used the same route of faunal interchange between the two continents (see Jerzykiewicz & Russell 1991 for citations).

In latest Cretaceous time, the family Teiidae experienced a sharp decline accompanying the major extinctions of terrestrial vertebrates through the K/T transition (Archibald & Bryant 1990; Sheehan & Fastovsky 1992). Lack of a Paleocene record of teiids in both Asia and North America has led several authors (Gorman 1970; Estes 1983b; Fox 1989) to postulate that the family vanished from the northern continents at the end of the Cretaceous. If so, the Miocene record of Cnemidophorus (Estes & Tihen 1964) from Nebraska may reflect a Cenozoic reinvasion of the group from the south, as previous authors have suggested. Nonetheless, some of the Cretaceous forms evidently dispersed south earlier to Central and South America, occupying desirable ecologic niches there and undergoing a Cenozoic Neotropical radiation.

GEOLOGICAL DISTRIBUTION AND EVOLUTIONARY CHANGES OF LATE CRETACEOUS LIZARDS IN WESTERN CANADA

In western Canada, Late Cretaceous lizard fossils were previously documented in scattered publications (see Introduction), but no synthetic studies have ever been attempted, largely owing to lack of fossil specimens. However, over the past 25 years collections from Alberta and Saskatchewan have provided important materials for undertaking the research reported in this paper. The purpose of this section is to summarize the fossil record of lizards from the Upper Cretaceous of western Canada, and to discuss the evolutionary changes through time of the relevant groups in the study area. The geological distribution of these lizards is summarized in the form of two charts (Text-figs. 28-29), in which the radiometric ages are from Harland et al. (1990), and Thomas et al. (1990). In the following discussion, I recognize three lizard assemblages on the basis of differences in geological age and taxonomic composition.

I. Aquilan (early Campanian) Lizard Assemblage

Aquilan, or early Campanian, lizard fossils are known in western Canada from the upper member of the Milk River Formation, southern Alberta. The Milk River assemblage (see Text-figs. 28-29) documents the earliest records for the families of Iguanidae, Scincidae, Xenosauridae, Necrosauridae, and the earliest certain record of the Anguidae; and it also includes several early teiids (Chamops, Sphenosiagon, and Glyptogenys).

Iguanidae: The Milk River iguanids include Cnephasaurus and an unnamed new genus and species. In tooth morphology Cnephasaurus closely resembles the Recent Crotaphytus collaris, a predatory crotaphytine found in Mexico and Central America. If this relationship is correctly recognized, this discovery indicates that the evolutionary history of the

Crotaphytinae (ranked as a family in Frost & Etheridge 1989) can be traced back to early Campanian time. The unnamed new genus and species is recognized on a more fragmentary specimen, and its relationship with other iguanids is unknown.

Scincomorpha: The Aquilan Teiidae are not as diverse as the Judithian and the Lancian teiids, with only three taxa (*Chamops* sp.?, *Sphenosiagon* *simplex*, and possible *Glyptogenys*) recognized from relatively extensive sampling by screen-washing. If not a result of taphonomic processes (taphonomic loss, see Wilson 1988), the paucity of teiids in the Aquilan assemblage may indicate that the diversification of the group did not take place until middle Campanian (Judithian) time.

The Scincidae are represented in the assemblage by two genera: first, *Pememabuya* shows a strong tendency in jaw construction and tooth morphology toward the Recent *Mabuya* group (which now has a nearly worldwide distribution), and may represent an early Campanian precursor of it. Second, *Aocnodromeus* is characterized by wrinkled enamel on the tooth crowns. The tooth form of this lizard indicates an affinity with the Scincidae, but a robust subdental shelf and a strong mandibular symphysis are equally indicative of cordylid affinities.

Anguimorpha: Both Xenosauridae and Anguidae are recorded by materials identified as "genus & species undetermined." However, both jugal and maxillary materials of the Xenosauridae are clearly distinguishable from those of *Exostinus*, indicating that Milk River early record may represent a new genus and species. The Anguidae are represented by dentary materials that clearly show synapomorphic character states for the family, especially formation of the dorsal and anterior border of the anterior inferior alveolar foramen by the dentary (Estes 1964; Estes et al. 1988). Previous to this study, an uncertain record of the Anguidae was reported from the Paluxy Formation, Texas (Winkler et al. 1990). However, the specimen figured (SMU 72297, see Winkler et al. 1990, fig. 8E) has a robust subdental shelf and a dental gutter; therefore, it is probably from a scincomorphan, not an anguid.

Accordingly, the Milk River specimens described in this paper document the earliest undoubted record for the Anguidae.

The Necrosauridae in this assemblage are recorded by an unnamed new genus and species, and fragmentary materials identified as "?Parasaniwa sp.." The unnamed new taxon shows similarites in tooth form and dentary morphology to the Lancian Coipodontosaurus cracens, and together with "?Parasaniwa sp.," the Milk River fossils document the earliest record for the family Necrosauridae. On the other hand, advanced varanoids (Helodermatidae and Varanidae) are absent from the Aquilan assemblage.

II. Judithian (middle Campanian) Lizard Assemblage

Scincomorpha: As shown in Text-fig. 28, scincomorphans in the mid-Campanian or Judithian assemblage in western Canada are predominantly represented by teiids. Members of the Scincidae and ?Cordylidae also occur in the assemblage, while fossils of the Iguanidae, known from both Aquilan and Lancian assemblages, are undiscovered in the Judithian. Contrary to the conclusions of previous authors (Sahni 1972; Armstrong-Ziegler 1980; Sullivan 1981; Estes 1983a), Judithian teiids are taxonomically different from those of Lancian age (see Estes 1964, 1983a; Estes et al. 1969), resembling in that respect the mammals, which have fewer than 10 % of the species in common between Judithian and Lancian horizons (see Lillegraven & McKenna 1986). The taxonomic diversity of the Teiidae (represented by at least 7 species in 6 genera) indicates an important pre-Lancian diversification of the family, and hence, reflects a significant episode in the evolutionary history of teiids (Gao & Fox 1991).

Anguimorpha: Judithian anguimorphan lizards are better documented than those in the Aquilan assemblage, and are represented by the Xenosauridae, Anguidae, Necrosauridae, Helodermatidae, and Varanidae. The evolutionarily important taxon Odaxosaurus (see Meszoely 1970; Sullivan 1982, 1986a-b; Estes 1983a) makes its earliest discovered occurrence in the Oldman Formation, and is represented by a new species, Odaxosaurus priscus, which closely resembles the Lancian O. piger, but differs from the latter in having a more robustly built dentary with fewer, less truncate, and barely striated teeth, and in having the ventral border of the intramandibular septum extending anteriorly of the midpoint of the tooth row. Parasaniwa (Necrosauridae) is well-documented in terms of a large number of individuals (some 80 specimens), and both Helodermatidae and Varanidae first appear in North America in the Judithian assemblage.

Following the Judithian diversification of several lizard groups, there is a gap in the fossil record during the late Campanian and early Maestrichtian in western Canada. The only lizard taxon known from deposits of this age in the study area is a teiid (?Chamops sp.) from the Wapiti Formation at the Kleskun Hills, northwestern Alberta (see discussion of Chamops segnis). The gap may partially result from the transgression of the Bearpaw Sea that covered large areas in Alberta and Saskatchewan (see, e.g., Caldwell et al. 1978), and lack of knowledge of microvertebrate fossils from the late Campanian-early Maestrichtian Horseshoe Canyon Formation and its equivalents in the study area.

III. Lancian (late Maestrichtian) Lizard Assemblage

Lancian or late Maestrichtian lizards are known in western Canada from the Scollard Formation, central Alberta, and the Frenchman Formation, southwestern Saskatchewan. In taxonomic composition, this assemblage is generally similar to that from the Lance and Hell Creek formations of Wyoming and Montana, but it includes several new taxa, as well.

Iguanidae: The Iguanidae in this assemblage are represented by at least one (or more than one) species from the Frenchman Formation; these lizards have high-crowned, flared, tricuspid teeth, resembling those of the Recent Ctenosaura similis, a terrestrial, herbivorous iguanine found in Mexico and Central America (Etheridge & de Queiroz 1988; Mattison 1989).

Scincomorpha: Lancian Teiidae are diverse, and are represented by five genera, of which four (*Chamops*, *Leptochamops*, *Meniscognathus*, and *Haptosphenus*) are already known from the Lance and Hell Creek formations; one (*Stypodontosaurus*) is new, and so far only known from the Scollard Formation. The Scincidae are absent from the Lancian assemblage; this may indicate that the Scincidae underwent a decline in North America slightly earlier than the Teiidae. The Lancian assemblage also includes possible cordylids and two xantusiids (*Contogenys* and an unnamed new taxon), which are unknown from pre-Lancian horizons.

Anguimorpha: The Lancian anguimorphans from the study area include five genera in four families: *Exostinus* (Xenosauridae), *Odaxosaurus* (Anguidae), *Colpodontosaurus* and *Parasaniwa* (both in Necrosauridae), and *Paraderma* (Helodermatidae). All of these forms have been known previously from the type Lance Formation (see Estes 1964). The Varanidae are absent from the Lancian assemblage in western Canada.

IV. General Discussion on the Evolution of Late Cretaceous lizards in Western Canada

Iguania: For iguanians, the current known fossil record from western Canada (as well as from North America) consists exclusively of the Iguanidae, while in Asia the family was sympatric with the Agamidae in its early evolution (Gao & Hou 1992). This may indicate that the highly derived agamids (also chamaelonids) had an Old World origin, and may have never entered the New World after splitting from the Iguanidae.

The two earliest known iguanids from the Milk River Formation are both tricuspid in tooth morphology, and this tooth form of the Aquilan iguanids provides fossil evidence supporting the interpretation of Etheridge and de Queiroz (1988), who treated the tricuspid crown pattern as a primitive condition within iguanids. Etheridge and de Queiroz (ibid.) hypothesized two independent trends affecting crown pattern in iguanid evolution: one that included reduction and loss of lateral cusps, and a second marked by increasing cuspidation and broadening and flaring of the crowns. With the newly discovered fossils from the Upper Cretaceous of western Canada, the second trend can be corroborated, because the oldest known iguanids from the Milk River Formation show the more generalized, tricuspid condition, while iguanids from the geologically much younger Frenchman Formation have flared tooth crowns, with a much stronger separation of the lateral cusps from the prominent central cusp. On the other hand, the first trend of Etheridge and de Queiroz is not documented at all in the fossil record of early iguanids as currently known.

Scincomorpha: Within the suborder Scincomorpha, the family Teiidae have a much better fossil record than any of the other families. The family in terms of species diversity is obviously the most important group in the Late Cretaceous lizard fauna both in the study area and in nearby regions (e.g., Wyoming and Montana, see foregoing section).

Another scincomorphan family occurring in the Upper Cretaceous of western Canada is the Scincidae. This family is probably the most successful modern lizard group, as evidenced by its large number of species (probably around 1000 according to Mattison 1989) and worldwide distribution. The Scincidae are usually subdivided into four subfamilies (Greer 1970; Estes 1983a): Feyliniinae[2] Camp 1923 and Acontiinae Gray 1845 (both are restricted to Africa); Scincinae Gray 1925 (which are Old World, exclusive of Australia, in distribution); and Lygosominae Mittelman 1952 (which are worldwide and are the only subfamily occurring in both Australia and South America) (data from Greer 1970; Estes 1983a; Mattison 1989).

In spite of the great diversity and wide geographical distribution of Recent skinks, the family is poorly represented in the fossil record. There is no pre-Miocene fossil record in Asia, Africa, or Australia, where the Recent scincids are widespread. In North America, two genera, Contogenys and Sauriscus, were originally assigned to the Scincidae (Estes 1964,

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[2] Rieppel (1981) suggested revalidating the familial status of this group on their differences in skull and adductor musculature from other scincids.

1969b); however, as discussed in the preceding section on Xantusiidae, the former genus may have xantusiid affinities, while the latter could well be a cordylid, not a scincid (Estes 1983a-b). Accordingly, there is, in fact, no Mesozoic record known for the Scincidae previous to this study.

Some authors have suggested that the Scincidae had a biogeographic origin in Africa (Dunn 1936; Darlington 1957; Greer 1970) or in Asia (Estes 1983b). In this paper, with the discovery of the new skinks from the Milk River and Oldman formations, it seems clear that both the Scincinae and Lygosominae have Late Cretaceous precursors in western Canada, whereas the Old World origin hypothesis still lacks support from fossil evidence, as there is no Mesozoic fossil found in Africa or Asia.[3] Penemabuya from the Milk River Formation is morphologically a primitive Mabuya in the parts available for comparison. From this early Campanian structural ancestor to the Recent Mabuya group, the necessary evolutionary changes are: 1) further elongation of the dentary; 2) greater reduction and eventually loss of the subdental shelf; and 3) anterior closure of the Meckelian canal.

Two other scincomorphan families, Cordylidae and Xantusiidae, may also be documented in the fossil record from western Canada (or nearby areas). The uncertain referrals to these families of the fossil taxa described in this paper are largely because of lack of knowledge of the osteomorphology and natural history of the two groups. However, the newly discovered specimens described in this paper represent a beginning in the accumulation of fossil evidence for a better understanding of the evolutionary history of the two families.

Anguimorpha: Five anguimorphan families (Xenosauridae, Anguidae, Necrosauridae, Helodermatidae, and Varanidae) are well documented in the three fossil assemblages from western Canada. Xenosauridae first appear in the Aquilan assemblage, and also occur in the Judithian and Lancian assemblages. Although represented by fragmentary materials, this record certainly shows a trend in xenosaurid evolution involving widening and more extensive ornamentation of the jugal. The Anguidae have an early (probably the earliest known) record in the Aquilan assemblage, although they are represented by fragmentary specimens identified as "genus & species undetermined." The basal glyptosaurine anguid Odaxosaurus first occurs in the Judithian assemblage, and is documented there by a new species, which is clearly close to the type species, O. piger. A comparison of the Judithian species with O. piger reveals some morphological changes in the evolution of Odaxosaurus; these include shortening of the intramandibular septum and freeing of its ventral border, thickening of the crown enamel and more prominent striations. Odaxosaurus was originally founded on dentary materials (Gilmore 1928), but later work with added maxillaries, frontals and parietals has in some degree changed the diagnosis of the species and raised certain issues about the relationships of Odaxosaurus with glyptosaurine anguids (see, e.g., Estes 1983a; Sullivan 1986a-b; Gauthier 1984). Newly discovered maxillary and dentary specimens with osteoscutes from Lancian horizons show that disarticulated skull elements (frontals and parietals) may have been incorrectly associated with the maxillary and dentaries previously. However, a taxonomic revision of Odaxosaurus piger needs further study of better preserved jaw materials with osteoscutes.

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[3] Mimobecklesisaurus gansuensis Li 1985 from the Upper Jurassic Chijinpu Group, Gansu Province of China was reported as an early scincid, but is actually a paramacellodid (Gao & Hou in progress).

The Necrosauridae, an extinct family of primitive varanoid lizards, are represented in western Canada by Parasaniwa, Colpodontosaurus, and an unnamed new genus and species. Parasaniwa was probably quite common as the fossils of this lizard were widely distributed in North America through Campanian-Maestrichtian time. This predaceous lizard differs from Colpodontosaurus principally in having sharply pointed, trenchant teeth with basal infoldings, and in having a more prominent intramandibular septum. The Aquilan ?Parasaniwa sp. from the Milk River Formation is recognized on fragmentary dentaries with poorly preserved teeth; therefore, the tooth form and dentary morphology of this early necrosaurid are not clearly known yet, and its comparison with the congeneric form from the younger horizon is correspondingly limited. A Judithian new species of Parasaniwa is recognized (but unnamed owing to the difficulty in designating a holotype from currently known specimens), and it shows more primitive character states than the Lancian type species P. wyomingensis. A comparison of the two species reveals that two notable changes in Parasaniwa evolution are: 1) from a relatively straight condition, the dentary tooth-bearing border became more crescentic; and, 2) the parietal foramen shifted anteriorly from a posterior position, coupled with more extensive fusion of the osteoscutes on the dorsal surface of the parietal. Nonetheless, the basic tooth morphology (trenchant blade without serrations and simple basal infoldings) and the condition of the intramandibular septum (fused to the floor of the Meckelian canal) remained unchanged from Judithian to Lancian time.

The Helodermatidae were present in western Canada as early as Judithian (the family is also known from the Judith River Formation, Montana), and are well documented in Lancian deposits in central Alberta. Both Judithian and Lancian helodermatids retain primitive character states, such as a parietal foramen, and relatively greater number of teeth than Recent forms. However, Judithian Labrodioctes was substantially larger than Lancian Paraderma and does not have venom grooves on dentary teeth; Paraderma does have shallow venom grooves and appears to have been slightly larger than Recent Heloderma. These differences may suggest that a general trend in helodermatid evolution is the reduction of body size, accompanied by the development of the venom gland and grooves. Previous authors (Bogert & del Campo 1956; Pregill et al. 1986) have suggested that the venom gland and grooves of helodermatids were initially developed in a feeding context, but have secondarily assumed a function in defense. The large body size and robust teeth of the Judithian Labrodioctes certainly suggest that it was a more active predator than the Recent helodermatids. It is possible that during the evolution of helodermatids, the venom gland and grooves were developed late in the Late Cretaceous, associated with a change of feeding style and in compensation for loss in body size advantage.

The Varanidae have been known from western Canada for many years, since Gilmore (1923, 1928) first referred UA 112 (a dorsal vertebra) to the Lacertilia and subsequently named Palaeosaniwa canadensis. However, there have been disagreements concerning the familial assignment of this species (McDowell & Bogert 1954; Estes 1964, 1983a; Hoffstetter 1969), because P. canadensis has only been known with certainty from disarticulated vertebrae. Described in this paper for the first time, both maxillaries and dentaries of this species clearly show microserrations on the cutting edge of the teeth, supporting the referral of P. canadensis to the Varanidae. Palaeosaniwa canadensis marks the earliest appearance of the Varanidae in North America (Gilmore 1928; Estes 1983a), and may provide the earliest record of the family overall, depending on the actual age and relationships of Telmasaurus Gilmore 1943 from the Gobi Desert.

Text-fig. 28. Geological distribution of Late Cretaceous lizards in western Canada I. - Iguania + Scincomorpha.

Myr	Stage	NALM Age	Iguanidae	Teiidae	Scincidae	? Cordylidae	? Xantusiidae	Family incertae sedis
65	Maestrichtian	Lancian	Genus & species new (B)	Chamops Leptochamops Meniscognathus Haptosphenus Stypodontosaurus		Genus & species undetermined (B)	Genus & species new (unnamed) Contogenys	Genus & species new (A) Genus & species new (B)
	—?—	Edmontonian —?—		? Chamops sp.				
76	Campanian	Judithian		Socognathus Sphenosiagon Glyptogenys Gerontoseps Leptochamops Alocosaurus	Orthrioscincus	Genus & species undetermined (A)		Genus & species undetermined
83		Aquilan	Cnephasaurus Genus & species new (A)	Chamops sp.? Sphenosiagon Glyptogenys	Penemabuya Aocnodromeus			Genus & species undetermined

Text-fig. 29. Geological distribution of Late Cretaceous lizards in western Canada II. - Anguimorpha.

Myr	Stage	NALM Age	Xenosauridae	Anguidae	Necrosauridae	Helodermatidae	Varanidae
65	Maestrichtian	Lancian	*Exostinus*	*Odaxosaurus*	*Colpodontosaurus* *Parasaniwa*	*Paraderma*	
	—?—	Edmontonian					
76	Campanian	—?— Judithian	? *Exostinus* sp.	*Odaxosaurus*	*Parasaniwa* n. sp. (cf. *P. wyomingensis*)	*Labrodioctes* Genus & species undetermined	*Palaeosaniwa*
83		Aquilan	Genus & species undetermined	Genus & species undetermined	Genus & species new (unnamed) ? *Parasaniwa* sp.		

SUMMARY

1. The Upper Cretaceous non-marine deposits of western Canada have yielded fossil lizards representing some 40 species in more than 30 genera of 10 families. Hundreds of specimens collected from the Milk River, Oldman, Frenchman and Scollard formations reveal previously unknown aspects of the evolutionary history of the relevant lizard families during the last 18 Myr of the Cretaceous period in western Canada.

2. According to the differences in geological age and taxonomic composition, three fossil assemblages are recognizable: First, the Aquilan assemblage documents the earliest fossil record of the Iguanidae, Scincidae, Xenosauridae, Necrosauridae, and the earliest certain record of Anguidae; whereas the Teiidae are poorly recorded. Second, the Judithian assemblage reflects a major adaptive radiation of the Teiidae, and documents the earliest helodermatids and varanids in North America. Third, the Lancian assemblage is taxonomically similar to that previously known from the type Lance and Hell Creek formations, but includes several new taxa (especially of the Iguanidae) previously unknown from the latter formations.

3. The paucity of lizard fossil record during the late Campanian - early Maestrichtian in the main study area is probably partially the result of the transgression of the Bearpaw Sea, and partially owing to a general lack of knowledge of microvertebrate fossils from Edmontonian horizons.

4. The new discovery of Late Cretaceous iguanids from western Canada is especially significant, as it documents the earliest fossil record for the Iguanidae, and coupled with other discoveries from Central Asia, challenges the South American origin hypothesis and suggests a northern hemisphere origin of the family. The fossil evidence from western Canada also demonstrates that one of the evolutionary trends for the Iguanidae is from a generalized, primitive, tricuspid tooth form to an advanced, widely flared crown pattern.

5. Teiids are important components in the Late Cretaceous lizard fauna in North America. Current knowledge of the fossil record of the Teiidae supports the North American origin hypothesis of previous authors, and indicates that the family had a major radiation in both North America and Central Asia in middle Campanian time; but may have disappeared from northern continents at the K/T transition as previous authors have suggested. Probably also in Campanian time, some of the North American teiids dispersed to Central and South America, where they underwent a Cenozoic adaptive radiation.

6. The Scincidae were well-established in North America in Aquilan time, but may have never become as diverse as the Teiidae in the North American continent. Their absence in the Lancian assemblage may suggest that the group had declined in North America slightly earlier than the Teiidae.

7. Both Cordylidae and Xantusiidae may have a Late Cretaceous record in North America, but their evolutionary history remains poorly known because of poorly preserved specimens.

8. The Xenosauridae first appear in western Canada in the Aquilan assemblage, and the jugal may have tended to widen and become more extensively ornamented during their early evolution.

9. Although questionably reported from the Albian Paluxy Formation, Texas, the Anguidae definitely are present in the Milk River Formation in western Canada. New Odaxosaurus specimens from Judithian to Lancian horizons show an evolutionary increase in the striations on the tooth crowns, and shortening of the intramandibular septum. The new materials also indicate that previous workers may have incorrectly associated Lancian frontals and parietals with the maxillaries and dentaries (including the holotype) of Odaxosaurus.

10. Necrosauridae also first appear in the Aquilan assemblages, and are represented in the study area by Parasaniwa, Colpodontosaurus, and an unnamed new genus and species. In the evolution of Parasaniwa, the dentary becomes more slender and the tooth-bearing border

tends to become more crescentic; tooth form and the condition of the intramandibular septum show no changes from Judithian to Lancian time.

11. Both the Helodermatidae and the Varanidae are first known in North America in the Judithian lizard assemblage. For the Helodermatidae, a major evolutionary trend may have been the reduction of body size paralleling a change in feeding style. The development of venom grooves on the marginal teeth may have been a compensation for the loss of the advantage that large body size confers. *Palaeosaniwa canadensis* was founded on vertebral material, but knowledge of the species is now supplemented by maxillaries and dentaries; the presence of microserrations on the cutting edge of the marginal teeth, in combination with well-developed basal infoldings, confirms that *Palaeosaniwa canadensis* is an early (or the earliest known) member of the Varanidae.

Plate 1

Iguanidae, Cnephasaurus locustus n. gen. et sp., Milk River Formation, Alberta

Fig. 1. UALVP 29921 (holotype), incomplete right maxillary, lateral view. About X 12

Fig. 2. UALVP 29921, medial view. About X 12

Fig. 3. UALVP 33386, incomplete left maxillary, medial view. About X 12

Iguanidae, genus & species new (A), Milk River Formation, Alberta

Fig. 4. UALVP 29908, fragmentary left maxillary, lateral view. About X 12

Fig. 5. UALVP 29908, medial view. About X 12

Fig. 6. UALVP 29909, fragmentary left dentary, medile view. About X 12

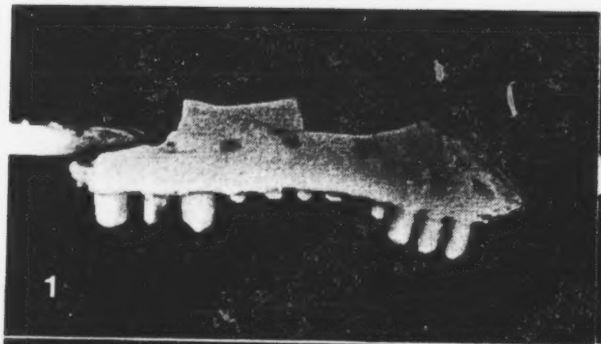
Iguanidae, genus & species new (B), Frenchman Formation, Saskatchewan

Fig. 7. SMNH P1927.916, fragmentary left dentary, medial view. About X 12

Fig. 8. SMNH P1927.885, fragmentary left dentary, medial view. About X 12

Fig. 9. SMNH P1927.998, fragmentary right dentary, medial view. About X 12

Fig. 10. SMNH P1927.980, fragmentary left dentary, medial view. About X 12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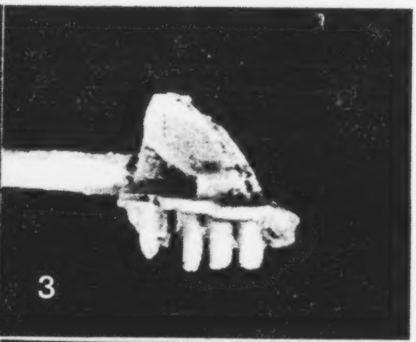
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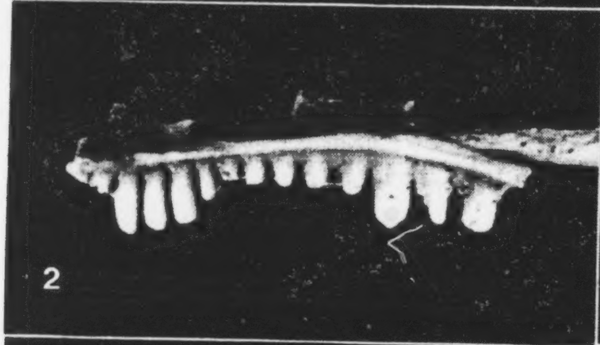
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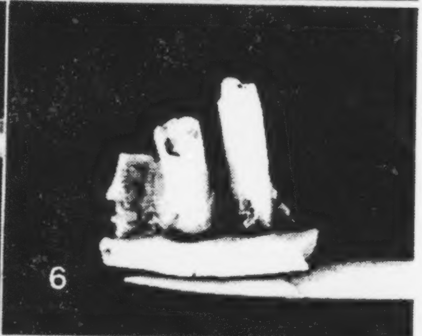
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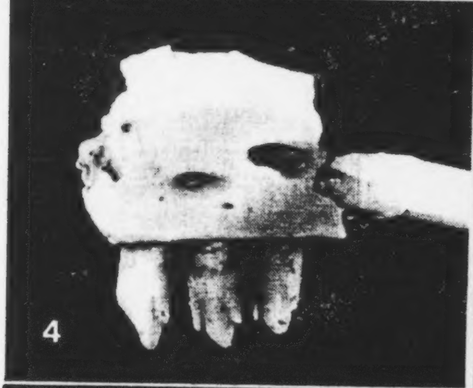
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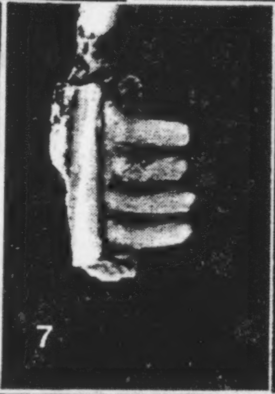
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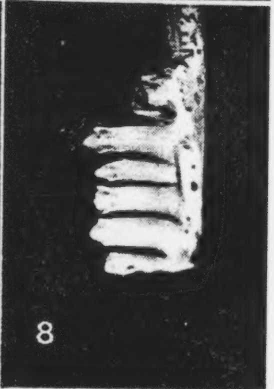
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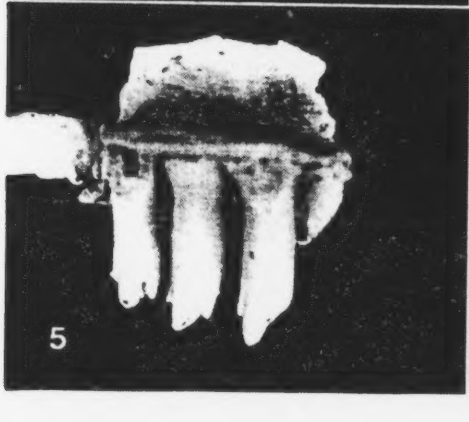
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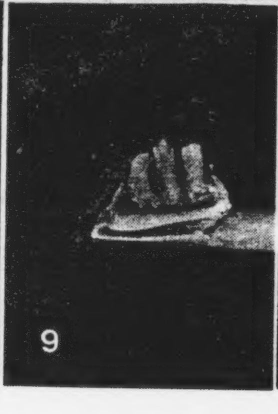
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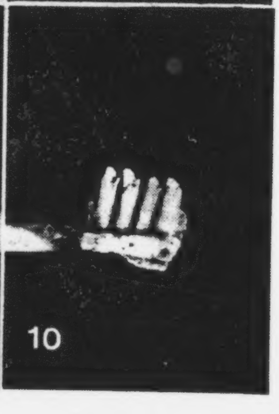
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Plate 2

Teiidae, Chamops segnis, Frenchman Formation, Saskatchewan

Fig. 1. SMNH P2004.86, incomplete left maxillary, medial view. About X 9

Fig. 2. SMNH P1927.824, incomplete left maxillary, medial view. About X 9

Fig. 3. SMNH P1927.874, incomplete left dentary, medial view. About X 9

Teiidae, Chamops segnis, Scollard Formation, Alberta

Fig. 4. UALVP 29841, incomplete maxillary, medial view. About X 9

Fig. 5. UALVP 29842, incomplete right dentary, medial view. About X 9

Teiidae, Chamops sp.?, Milk River Formation, Alberta

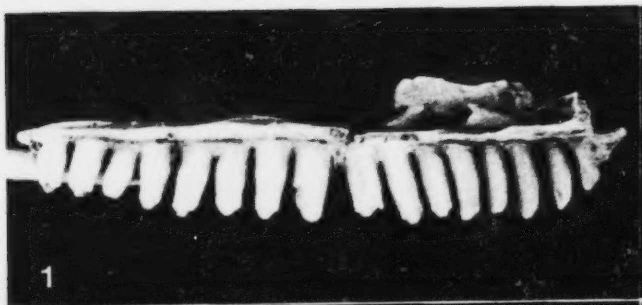
Fig. 6. UALVP 29816, incomplete left maxillary, medial view. About X 9

Fig. 7. UALVP 29817, incomplete right maxillary, medial view. About X 9

Fig. 8. UALVP 29826, incomplete left maxillary, medial view. About X 9

Fig. 9. UALVP 29819, fragmentary right dentary, medial view. About X 9

Fig. 10. UALVP 29820, incomplete left maxillary, medial view. About X 9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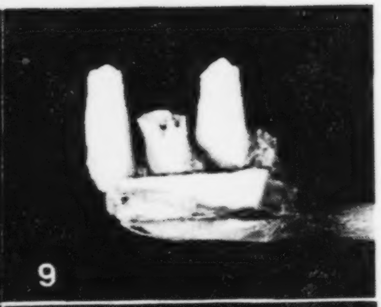
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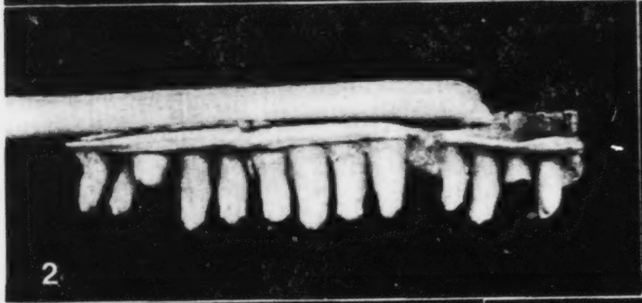
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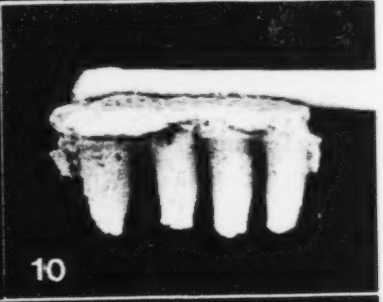
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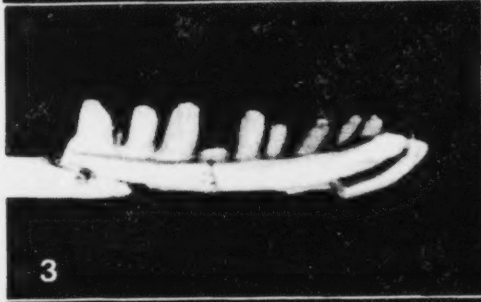
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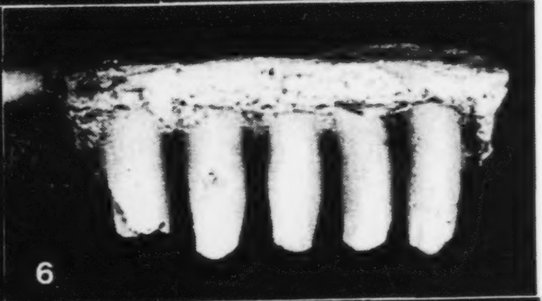
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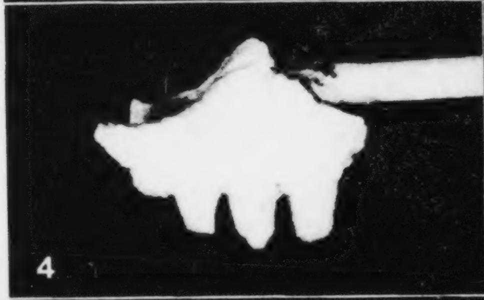
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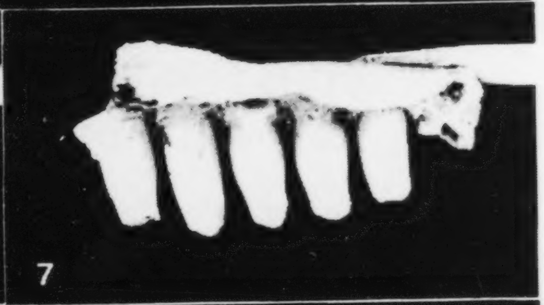
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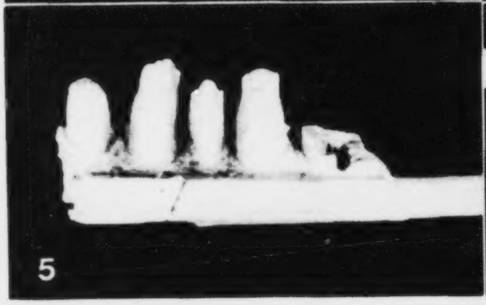
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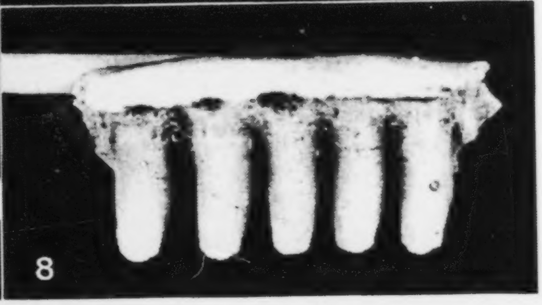
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Plate 3

Teiidae, Socognathus unicuspis, Oldman Formation, Alberta

Fig. 1. UALVP 29739 (holotype), incomplete left dentary, lateral view. About X 4

Fig. 2. UALVP 29739, medial view. About X 4

Fig. 3. UALVP 29736, incomplete left dentary, medial view. About X 4

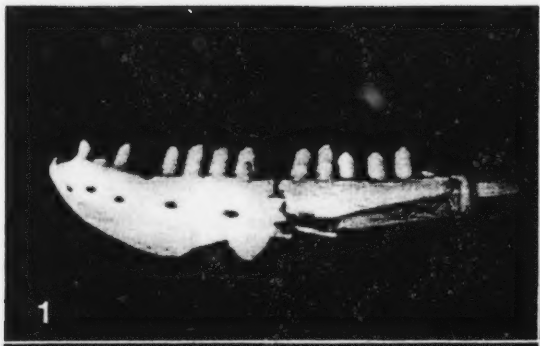
Fig. 4. UALVP 29910, incomplete right maxillary, medial view. About X 4

Fig. 5. UALVP 29911, incomplete left maxillary, medial view. About X 4

Fig. 6. UALVP 29743, incomplete right dentary, medial view. About X 7

Fig. 7. UALVP 29744, incomplete right dentary, medial view. About X 7

Fig. 8. RTMP 82.24.57, incomplete right dentary, medial view. About X 7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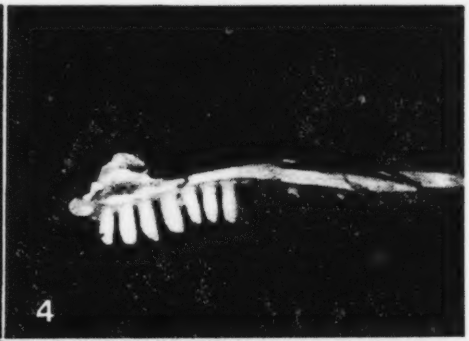
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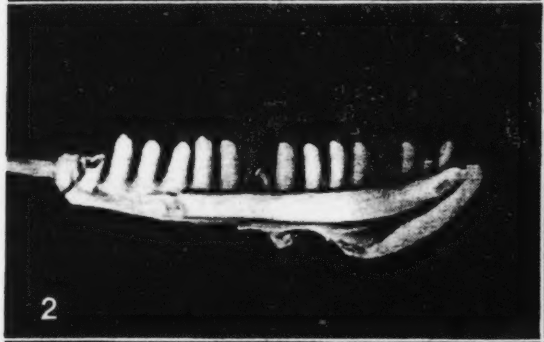
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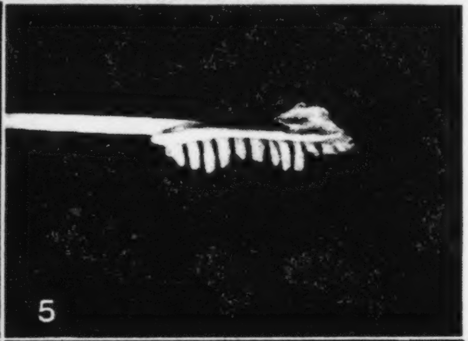
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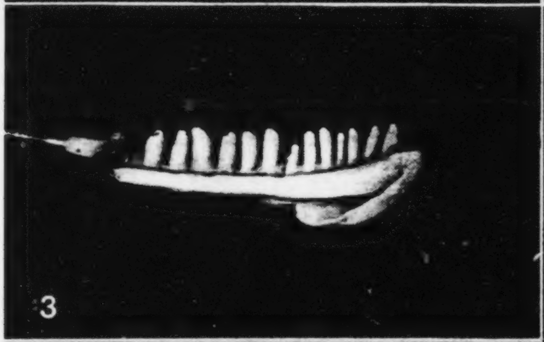
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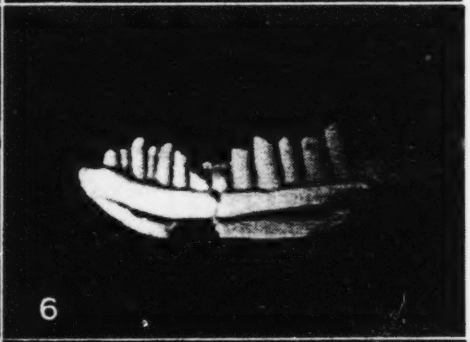
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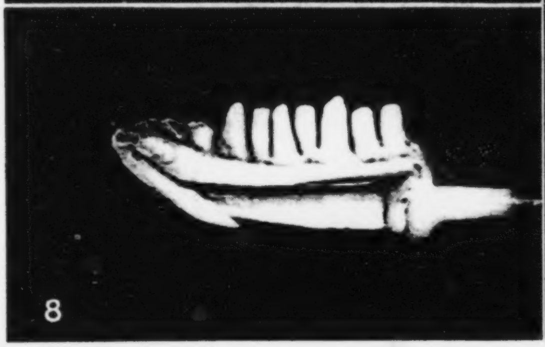
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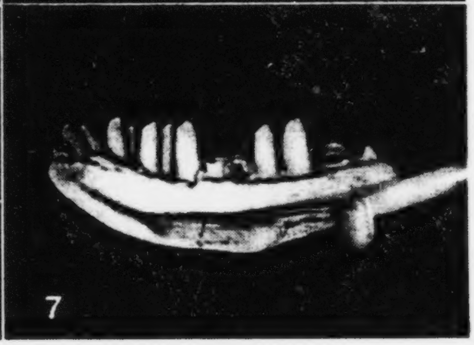
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Plate 4

Teiidae, Sphenosiagon simplex, Oldman Formation, Alberta

Fig. 1. UALVP 29742 (holotype), incomplete left mandible, lateral view. About X 8

Fig. 2. UALVP 29742, medial view. About X 8

Sphenosiagon simplex, Milk River Formation, Alberta

Fig. 3. UALVP 29836, incomplete right dentary, medial view. About X 7

Fig. 4. UALVP 29837, incomplete left dentary, medial view. About X 7

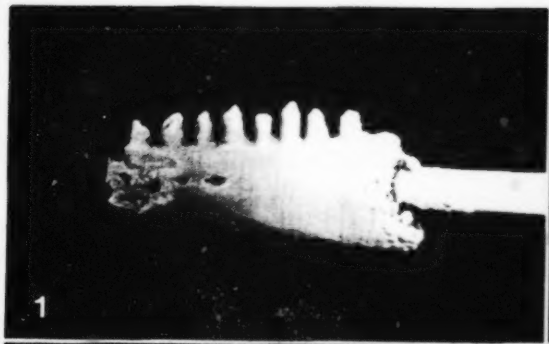
Teiidae, Glyptogenys ornata, Oldman Formation, Alberta

Fig. 5. UALVP 29735 (holotype), incomplete left dentary, lateral view. About X 7

Fig. 6. UALVP 29735, medial view. About X 7

Fig. 7. UALVP 29913, incomplete right dentary, lateral view. About X 7

Fig. 8. UALVP 29913, medial view. About X 7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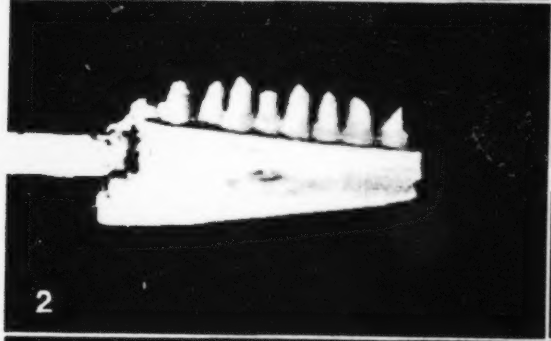
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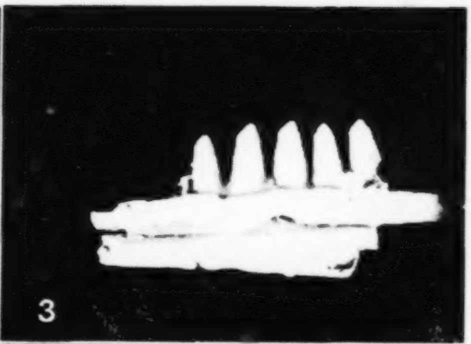
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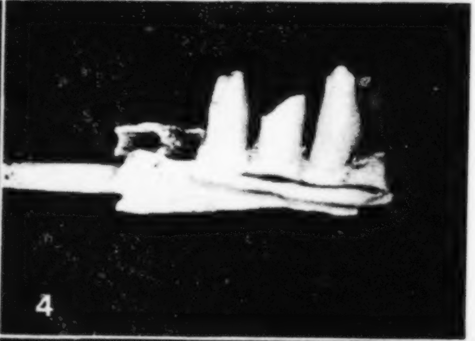
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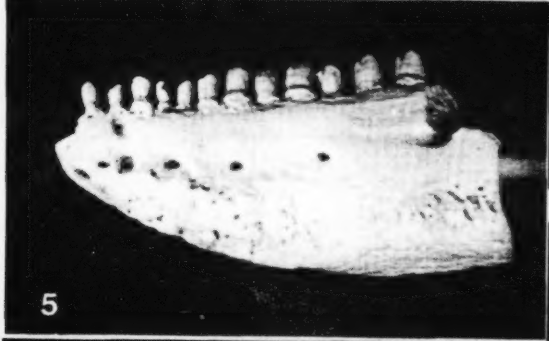
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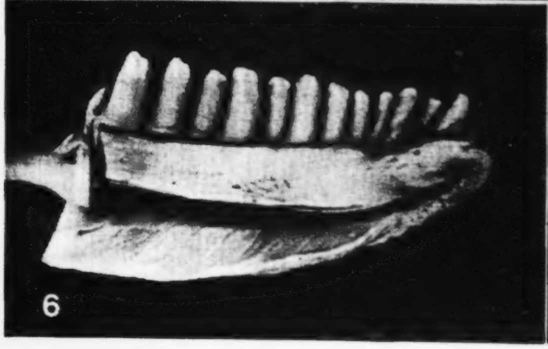
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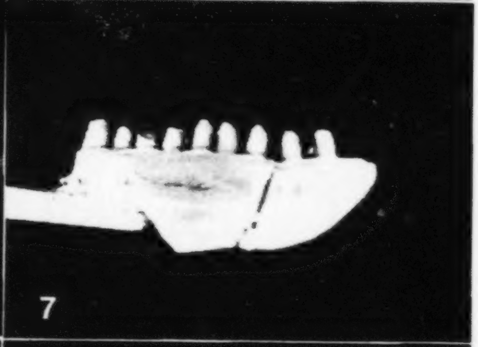
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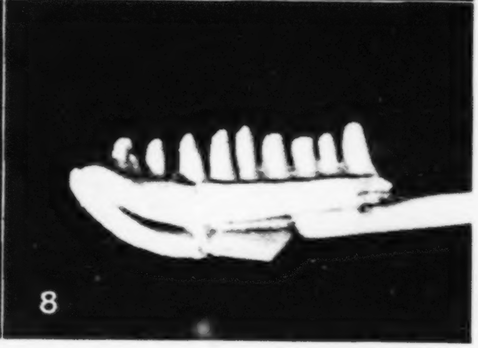
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Plate 5

Teiidae, Gerontoseps irvinensis, Oldman Formation, Alberta

Fig. 1. UALVP 29754 (holotype), incomplete right mandible, lateral view. About X 9

Fig. 2. UALVP 29754, medial view. About X 9

Fig. 3. UALVP 29760, incomplete left dentary, medial view. About X 9

Fig. 4. UALVP 29761, incomplete left dentary, medial view. About X 9

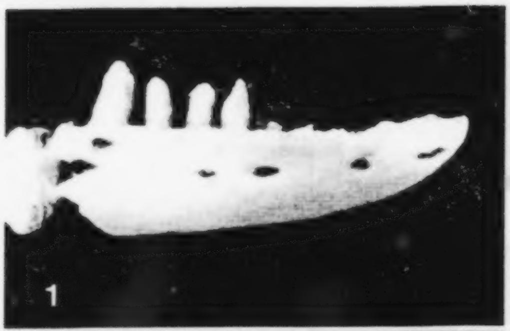
Teiidae, Leptochamops denticulatus, Frenchman Formation, Saskatchewan

Fig. 5. SMNH P1927.231, incomplete left maxillary, medial view. About X 12

Fig. 6. SMNH P1927.893, incomplete left dentary, medial view. About X 12

Fig. 7. SMNH P2004.89, incomplete left maxillary, lateral view. About X 12

Fig. 8. SMNH P2004.89, medial view. About X 12



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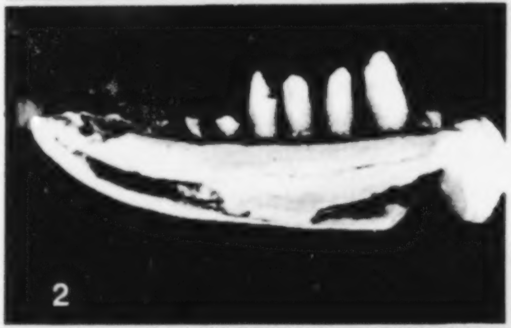

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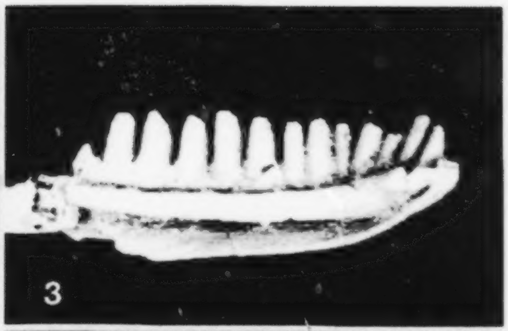

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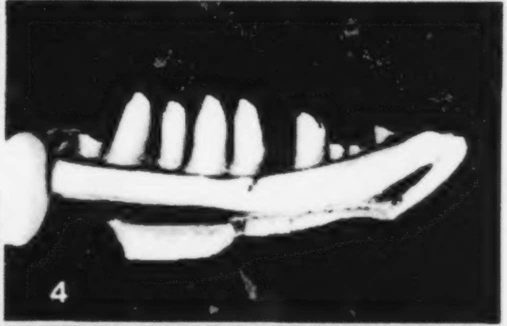

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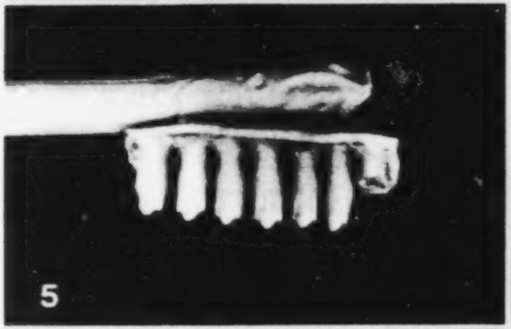

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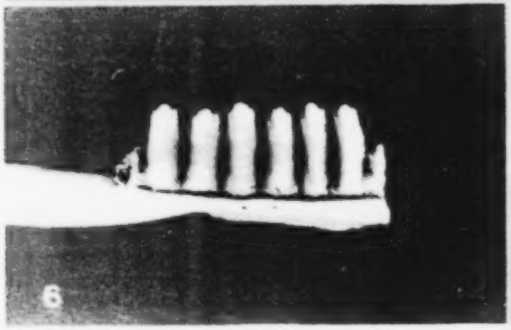

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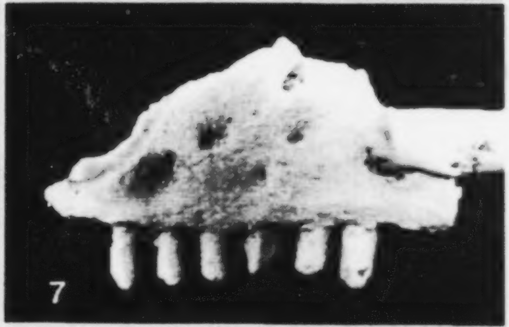

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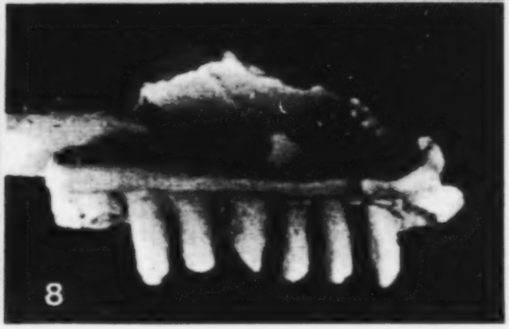

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Plate 6

Teiidae, Leptochamops thrinax, Oldman Formation, Alberta

Fig. 1. UALVP 29749 (holotype), incomplete left dentary, lateral view. About X 8

Fig. 2. UALVP 29749, medial view. About X 8

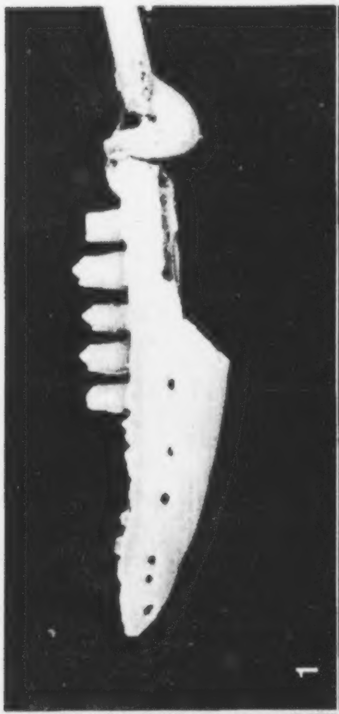
Fig. 3. UALVP 29748, incomplete left dentary, medial view. About X 8

Fig. 4. UALVP 29753, incomplete left dentary, medial view. About X 8

Leptochamops sp. (cf. L. denticulatus), Oldman Formation, Alberta

Fig. 5. UALVP 29772, nearly complete right dentary, medial view. About X 8

Fig. 6. UALVP 29741, incomplete right dentary with splenial, medial view. About X 8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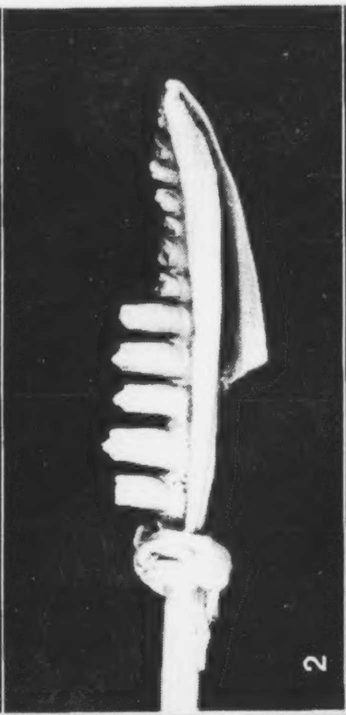
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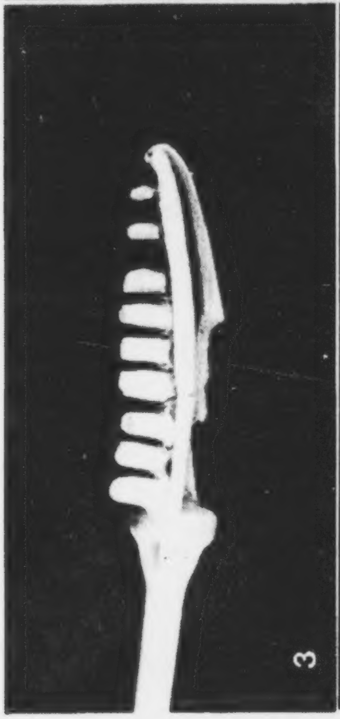
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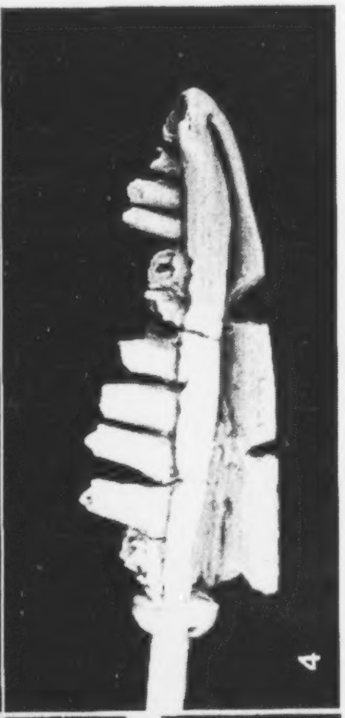
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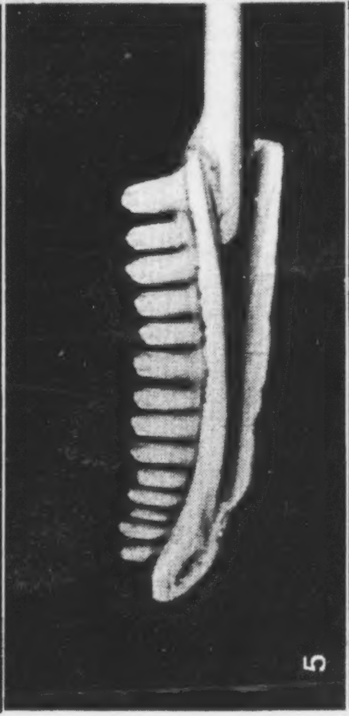
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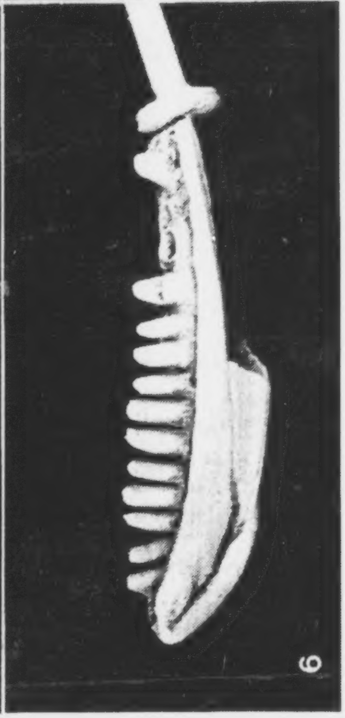
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Plate 7

Teiidae, Meniscognathus altmani, Frenchman Formation, Saskatchewan

Fig. 1. SMNH P1927.900, incomplete left maxillary, medial view. About X 12

Fig. 2. UALVP 29833, incomplete left maxillary, medial view. About X 12

Fig. 3. SMNH P1927.903, incomplete right dentary, medial view. About X 12

Fig. 4. SMNH P1927.887, incomplete left dentary, medial view. About X 12

Meniscognathus altmani, Lance and Hell Creek formations, Wyoming and Montana

Fig. 5. UALVP 29774, nearly complete left dentary, medial view. About X 8

Fig. 6. UALVP 29775, incomplete right maxillary, medial view. About X 12

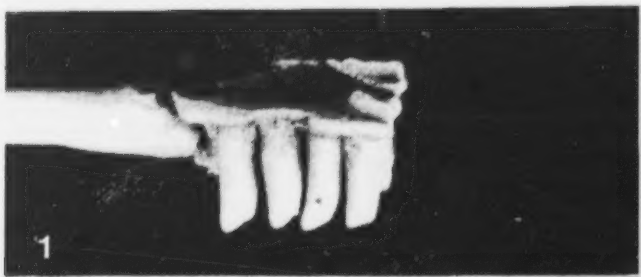
Teiidae, Haptosphenus placodon, Frenchman and Scollard formations,
Saskatchewan and Alberta

Fig. 7. SMNH P1920.23, incomplete left mandible, medial view. About X 8

Fig. 8. UALVP 33921, incomplete left mandible, medial view. About X 8

Fig. 9. UALVP 29780, incomplete right mandible, medial view. About X 8

Fig. 10. UALVP 29771, incomplete right mandible, medial view. About X 8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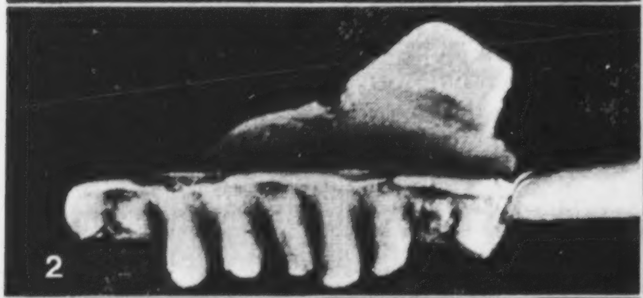
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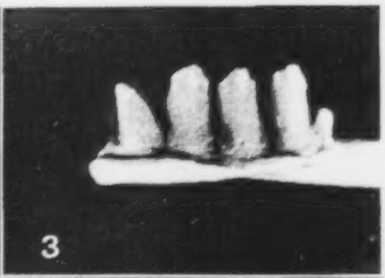
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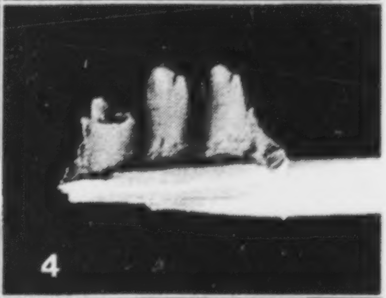
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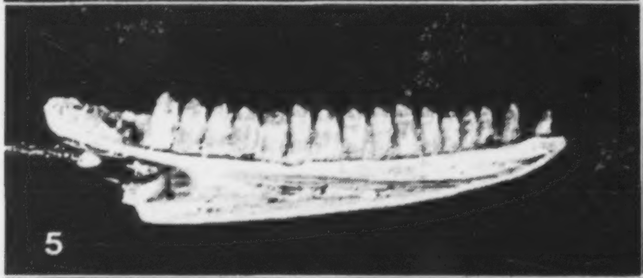
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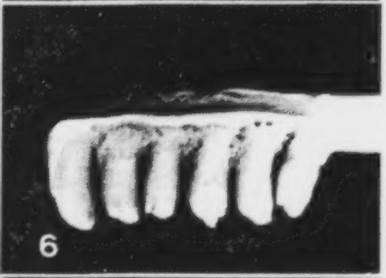
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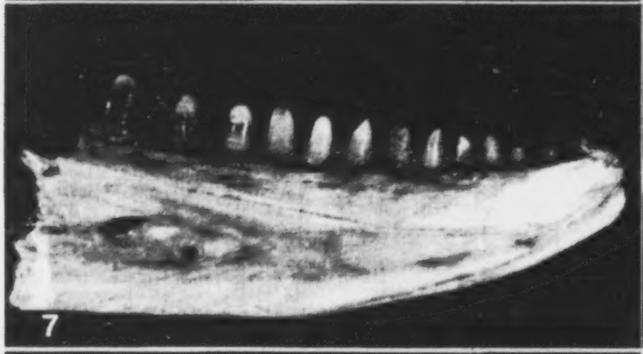
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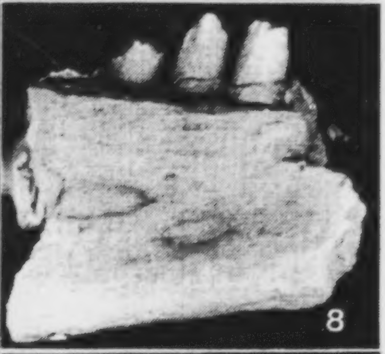
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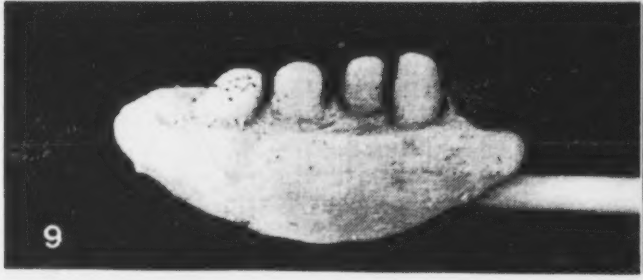
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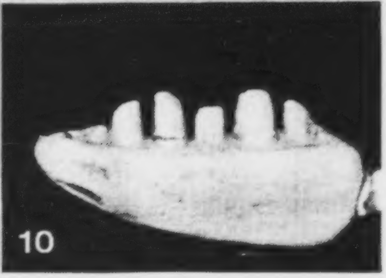
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Plate 8

Teiidae, Stypodontosaurus melletes n. gen. et sp., Scollard Formation, Alberta

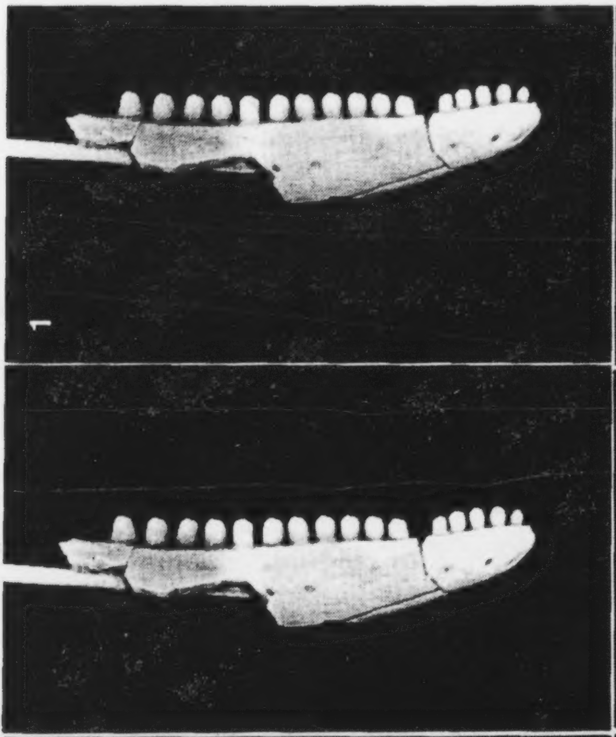
Fig. 1. UALVP 29844 (holotype), incomplete right dentary (stereophotographic pair), lateral view. About X 4

Fig. 2. UALVP 29844 (stereophotographic pair), medial view. About X 4

Teiidae, Alocosaurus johnstoni n. gen. et sp., Oldman Formation, Alberta

Fig. 3. UALVP 29791 (holotype), incomplete right dentary (stereophotographic pair), lateral view. About X 6

Fig. 4. UALVP 29791 (stereophotographic pair), medial view. About X 6



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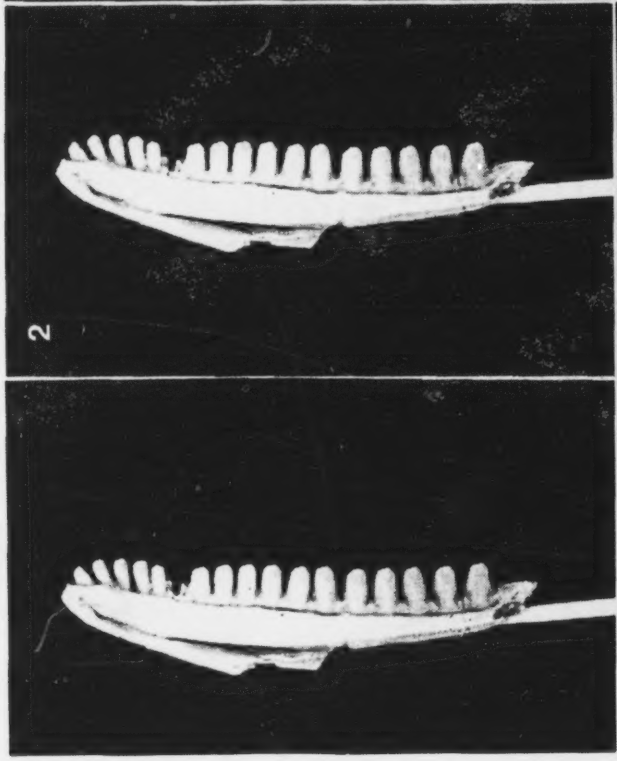

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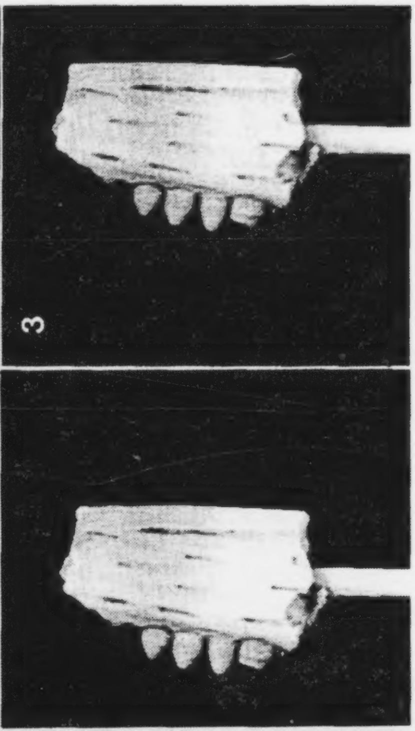

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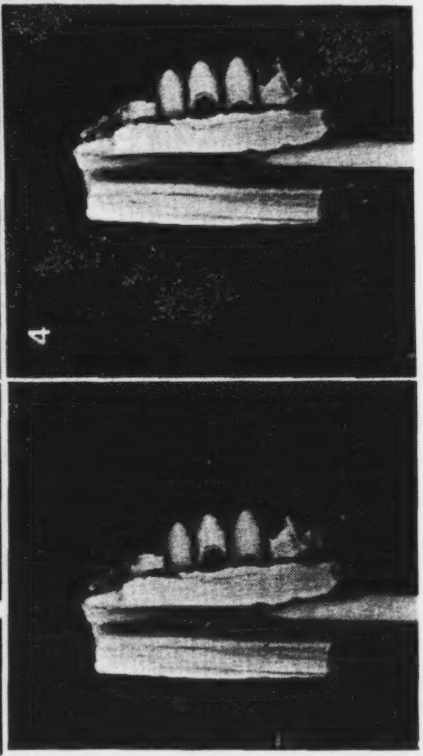

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Plate 9

Scincidae, *Penemabuya antecessa* n. gen. et sp., Milk River Formation, Alberta

Fig. 1. UALVP 29789 (holotype), incomplete right dentary, lateral view. About X 6

Fig. 2. UALVP 29789, medial view. About X 6

Fig. 3. UALVP 29788, incomplete right dentary, medial view. About X 6

Scincidae, *Orthrioscincus mixtus* n. gen. et sp., Oldman Formation, Alberta

Fig. 4. UALVP 29747 (holotype), incomplete left dentary, lateral view. About X 6

Fig. 5. UALVP 29747, medial view. About X 6

Fig. 6. UALVP 29904, incomplete right dentary, medial view. About X 6

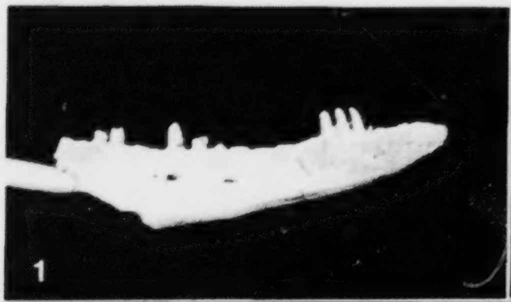
Scincidae, *Acnodromeus corrugatus* n. gen. et sp., Milk River Formation, Alberta

Fig. 7. UALVP 29905 (holotype), nearly complete left dentary, lateral view. About 6

Fig. 8. UALVP 29905, medial view. About X 6

Fig. 9. UALVP 29906, incomplete left dentary, lateral view. About X 6

Fig. 10. UALVP 29906, medial view. About X 6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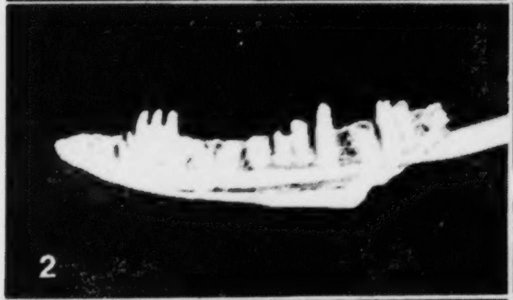
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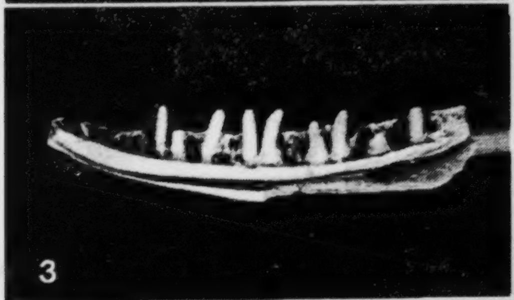
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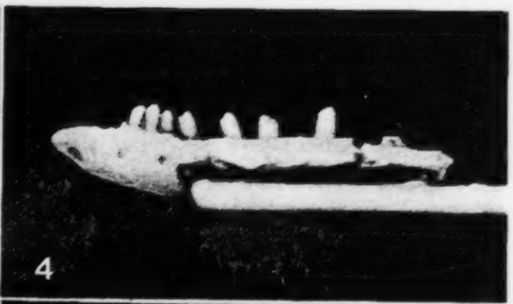
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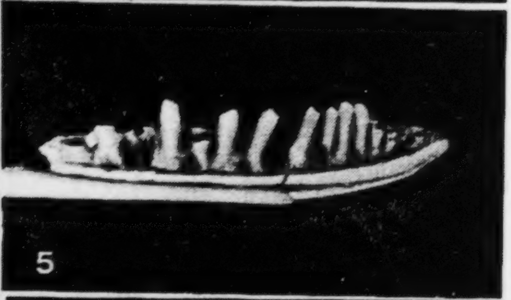
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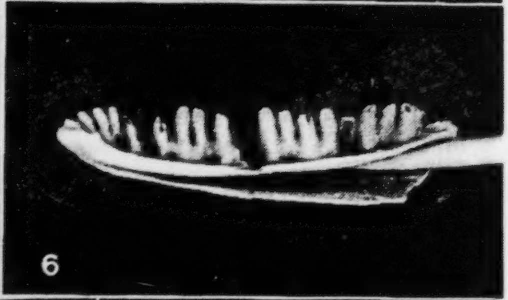
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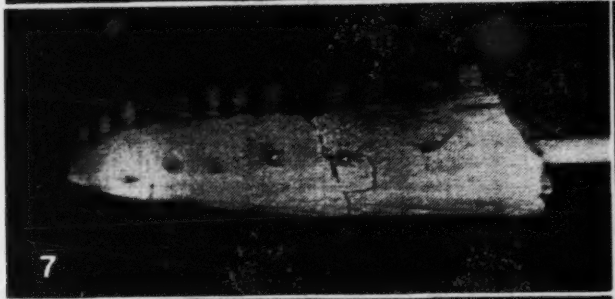
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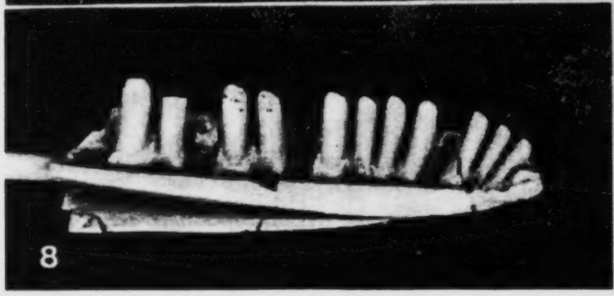
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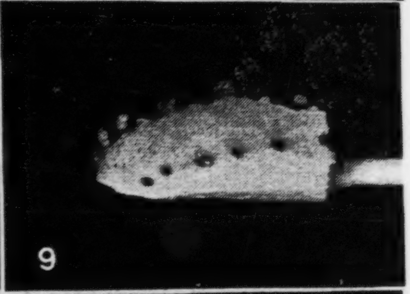
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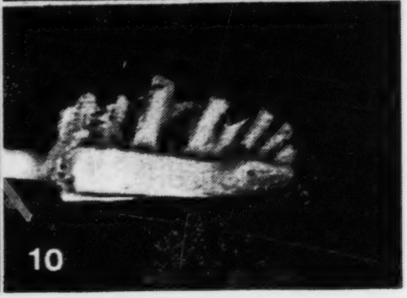
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Plate 10

?Cordylidae, genus & species undetermined (A), Oldman Formation, Alberta

Fig. 1. UALVP 29810, incomplete right dentary, medial view. About X 9

Fig. 2. UALVP 29907, incomplete right dentary, medial view. About X 9

?Cordylidae, genus & species undetermined (B), Hell Creek Formation, Montana

Fig. 3. UALVP 29722, incomplete left dentary, medial view. About X 9

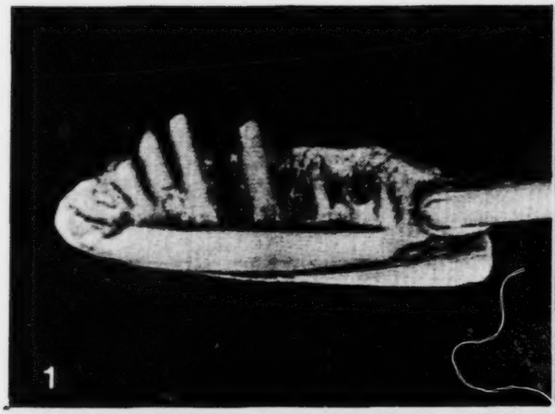
?Xantusiidae, genus & species new (unnamed), Hell Creek Formation, Montana

Fig. 4. UALVP 29840, incomplete right mandible, medial view. About X 9

?Xantusiidae, *Contogenys sloani*, Hell Creek Formation, Montana

Fig. 5. UALVP 29839, incomplete right mandible, lateral view. About X 9

Fig. 6. UALVP 29839, medial view. About X 9



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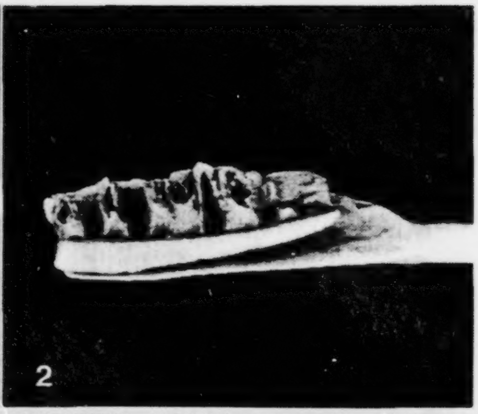

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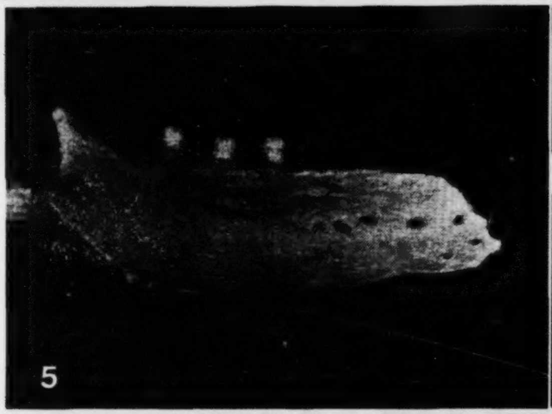

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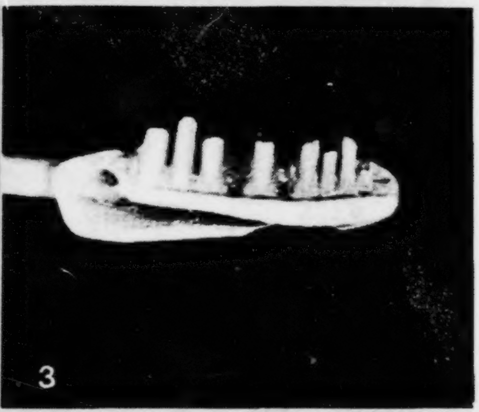

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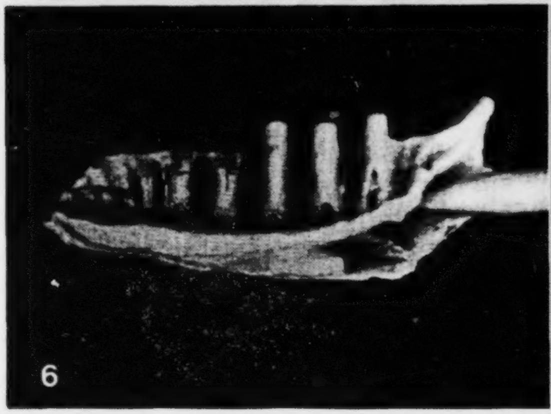

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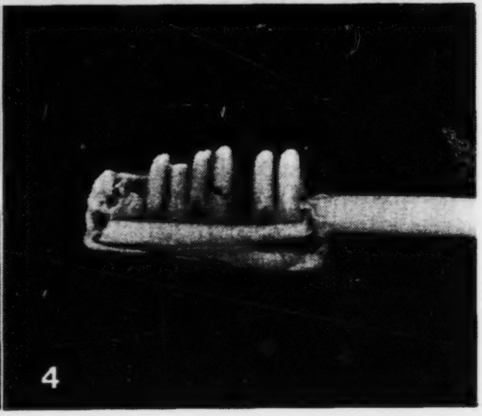

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Plate 11

Family incertae sedis, genus & species new (A), Frenchman Formation, Saskatchewan

Fig. 1. SMNH P1927.880, incomplete right dentary, medial view. About X 10

Genus & species new (B), Frenchman Formation, Saskatchewan

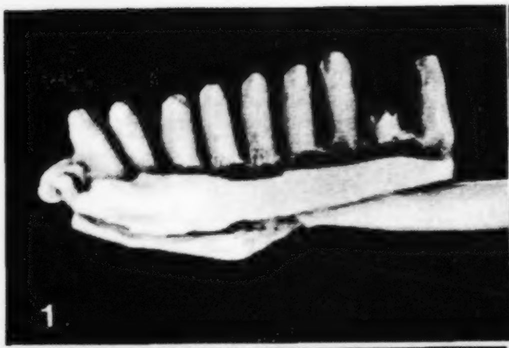
Fig. 2. SMNH P1927.886, incomplete left dentary, medial view. About X 10

Fig. 3. SMNH P2004.90, left dentary (stereophotographic pair), medial view. About X 10

Genus & species undetermined, Milk River and Oldman formations, Alberta

Fig. 4. UALVP 29830, incomplete right maxillary, medial view. About X 10

Fig. 5. RTMP 85.36.275, incomplete left dentary, medial view. About X 10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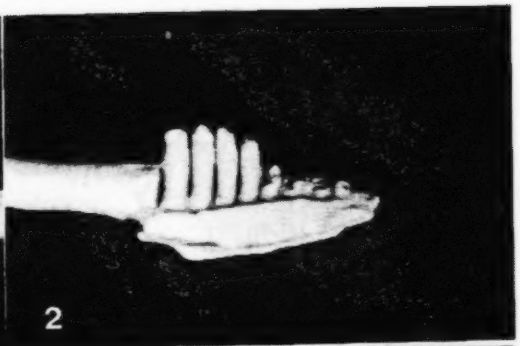
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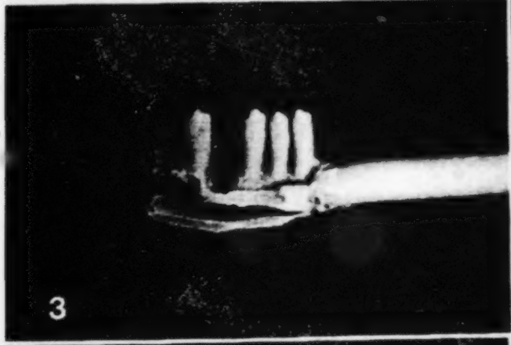
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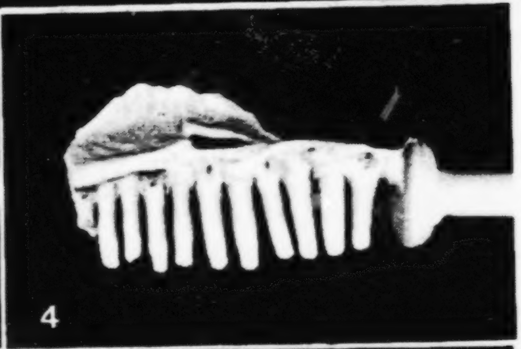
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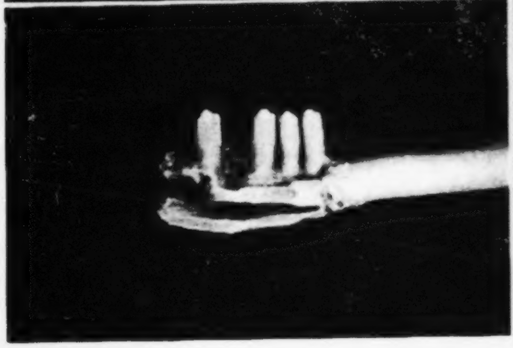

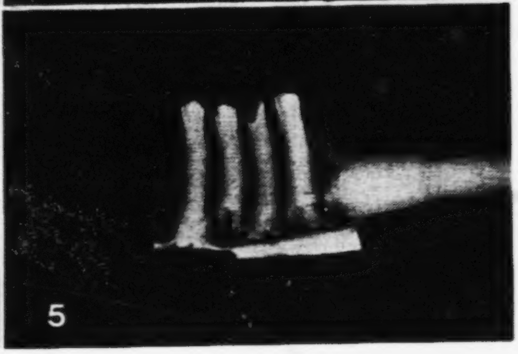
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Plate 12

Xenosauridae, Exostinus lancensis, Lance and Hell Creek formations,
Wyoming and Montana

Fig. 1. UALVP 29849, incomplete right maxillary, lateral view. About X 7

Fig. 2. UALVP 29850, incomplete left maxillary, medial view. About X 7

Fig. 3. UALVP 29919, incomplete frontal, dorsal view. About X 7

Fig. 4. UALVP 29838, nearly complete left dentary, medial view. About X 7

Fig. 5. UALVP 29920, left jugal, lateral view. About X 5

Fig. 6. UALVP 29847, incomplete parietal dorsal view. About X 7

Xenosauridae, ?Exostinus sp., Oldman Formation, Alberta

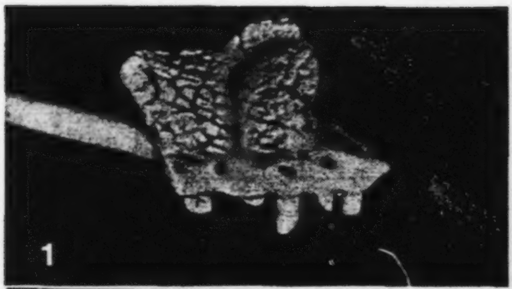
Fig. 7. UALVP 944, incomplete frontal, dorsal view. About X 7

Xenosauridae, genus & species undetermined, Milk River Formation, Alberta

Fig. 8. UALVP 29914, incomplete right jugal, lateral view. About X 7

Fig. 9. UALVP 29915, incomplete left maxillary, lateral view. About X 7

Fig. 10. UALVP 29917, incomplete right maxillary, medial view. About X 7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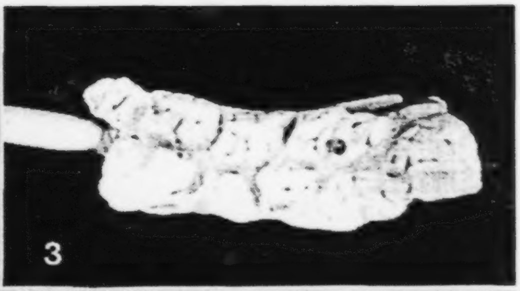
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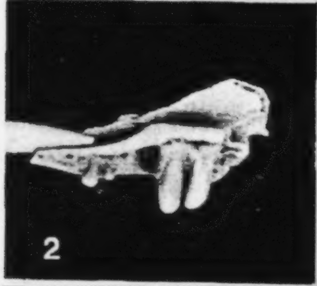
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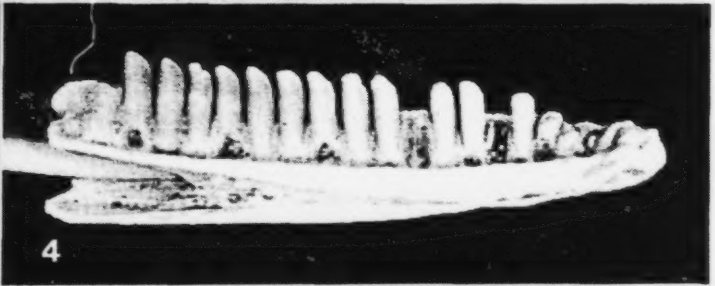
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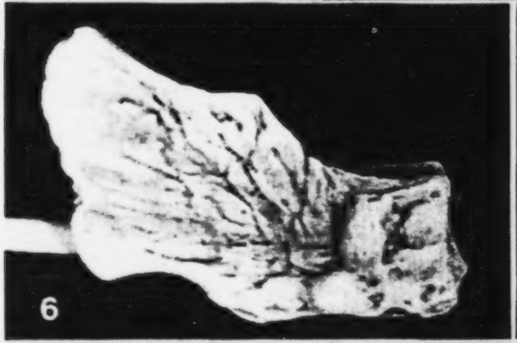
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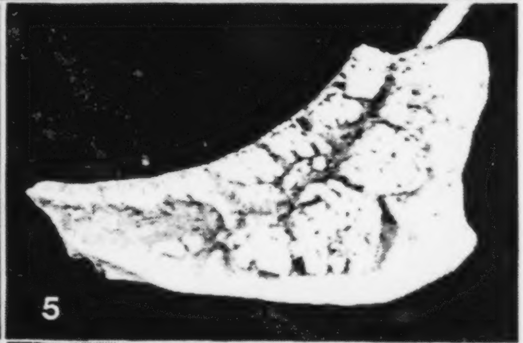
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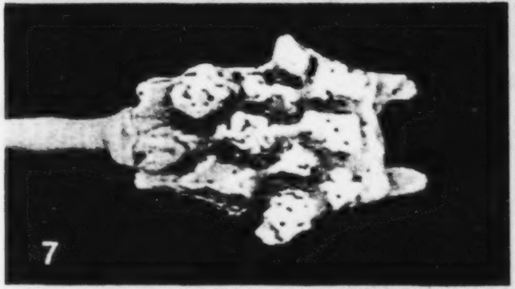
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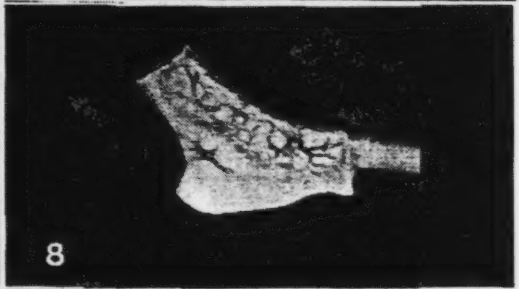
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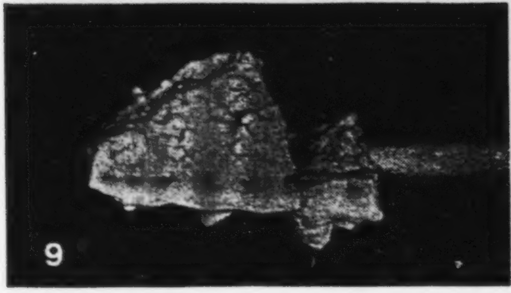
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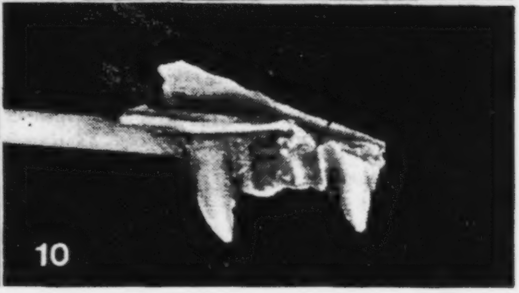
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Plate 13

Anguidae, Odaxosaurus piger, Scollard (Alberta), Frenchman (Saskatchewan) and Lance (Wyoming) formations

Fig. 1. UALVP 33381, incomplete left dentary, medial view. About X 6.5

Fig. 2. UALVP 29851, incomplete right maxillary, medial view. About X 6.5

Fig. 3. UALVP 33382, incomplete left maxillary, medial view. About X 6.5

Fig. 4. UALVP 29852, nearly complete left dentary, medial view. About X 6.5

Odaxosaurus priscus n. sp., Oldman Formation, Alberta

Fig. 5. UALVP 29896 (holotype), incomplete right dentary, medial view. About X 6.5

Fig. 6. UALVP 29897, incomplete right dentary, medial view. About X 6.5

Fig. 7. UALVP 29892, right maxillary, medial view. About X 6.5

Fig. 8. UALVP 33380, fragmentary right dentary, medial view. About X 6.5

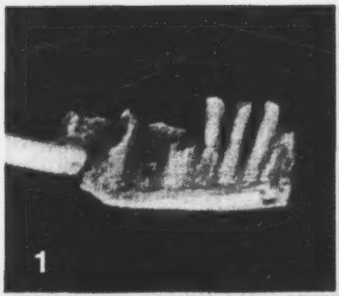
Fig. 9. UALVP 29891, left maxillary, medial view. About X 6.5

Fig. 10. UALVP 29894, fragmentary right maxillary, medial view. About X 6.5

Anguidae, genus & species undetermined, Milk River Formation, Alberta

Fig. 11. UALVP 33378, incomplete left dentary, medial view. About X 6.5

Fig. 12. UALVP 33379, fragmentary left dentary, medial view. About X 6.5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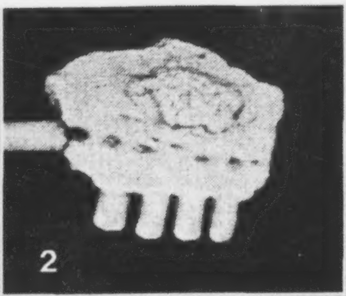
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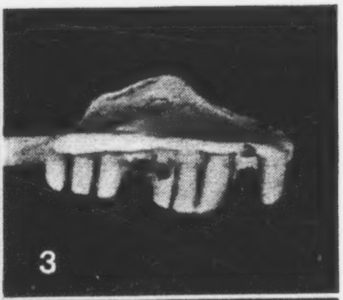
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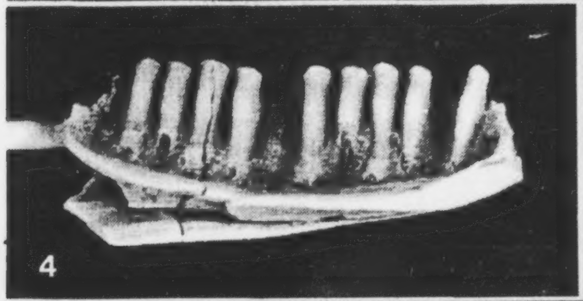
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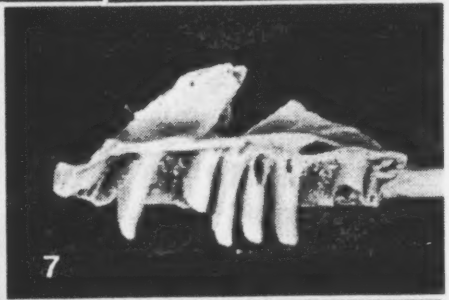
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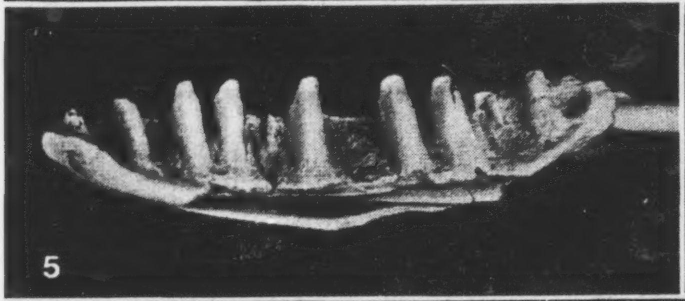
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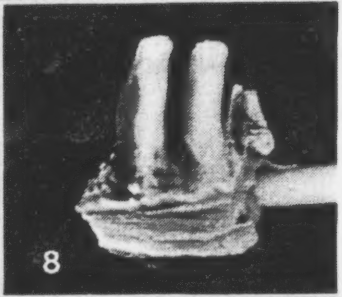
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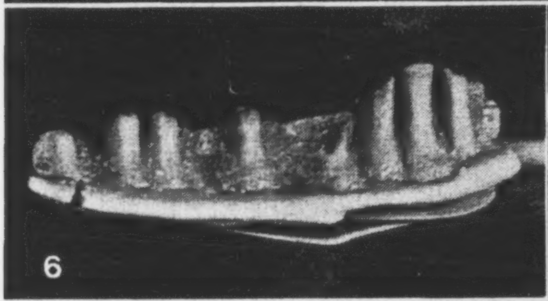
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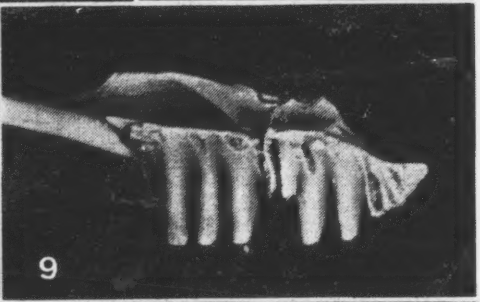
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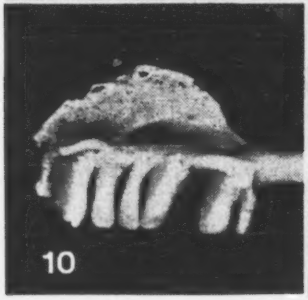
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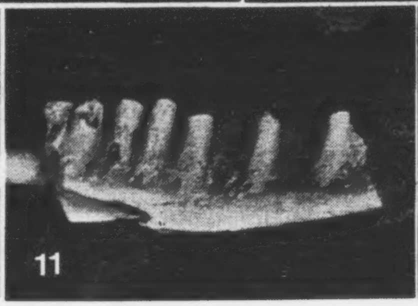
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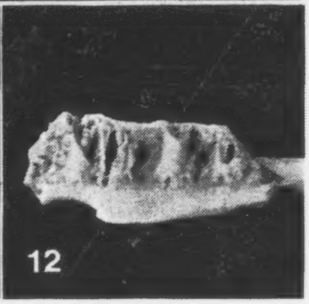
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Plate 14

Necrosauridae, Colpodontosaurus cracens, Scollard and Lance formations, Alberta and Wyoming

Fig. 1. UALVP 33388, fragmentary left dentary, medial view. About X 3.5

Fig. 2. UALVP 29781, left dentary, medial view. About X 3.5

Fig. 3. UALVP 29782, fragmentary right dentary, medial view. About X 3.5

Necrosauridae, genus & species new (unnamed), Milk River Formation, Alberta

Fig. 4. UALVP 29787, incomplete right dentary, medial view. About X 11

Fig. 5. UALVP 33383, right dentary, medial view. About X 11

Necrosauridae, Parasaniwa wyomingensis, Lancian formations in Alberta, Saskatchewan and Wyoming

Fig. 6. UALVP 33384, right maxillary, medial view. About X 6

Fig. 7. UALVP 33349, incomplete left dentary, medial view. About X 6

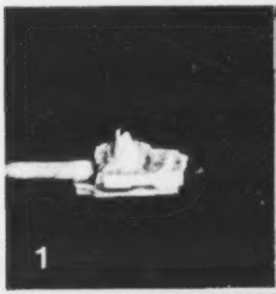
Fig. 8. UALVP 33361, incomplete left dentary, medial view. About X 6

Fig. 9. UALVP 33362, pterygoid, ventral view. About X 6

Fig. 10. UALVP 33354, right frontal, dorsal view. About X 6

Fig. 11. UALVP 33350, dorsal vertebra, dorsal view. About X 6

Fig. 12. UALVP 33350, ventral view. About X 6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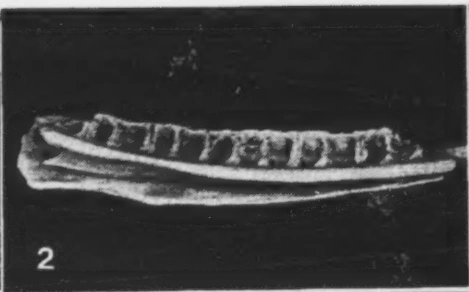
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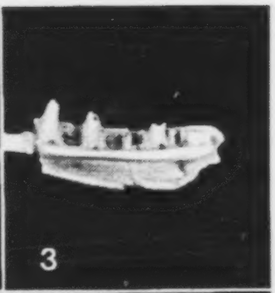
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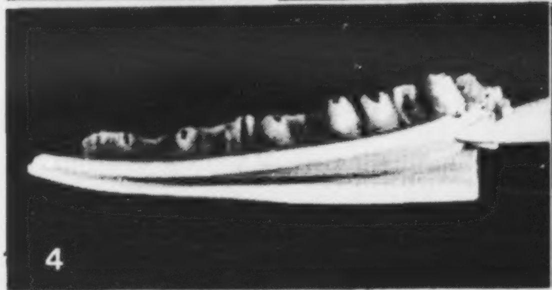
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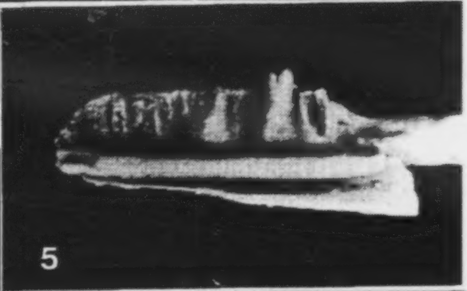
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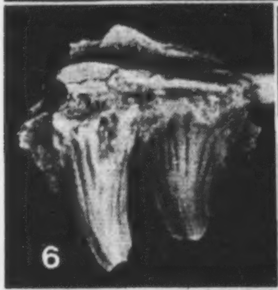
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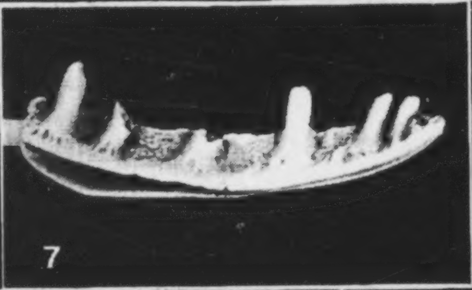
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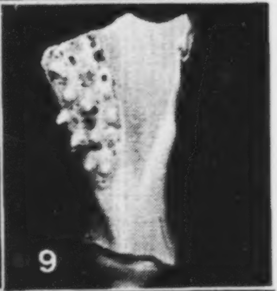
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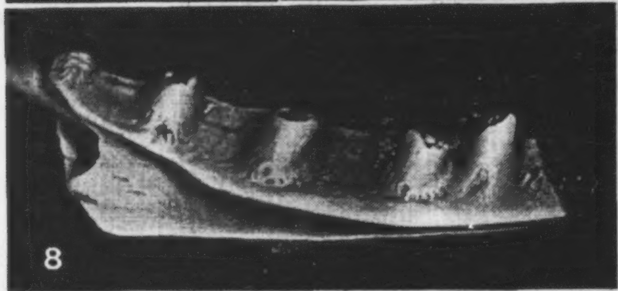
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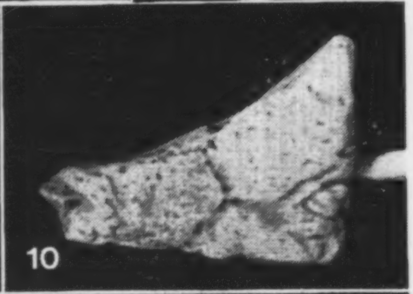
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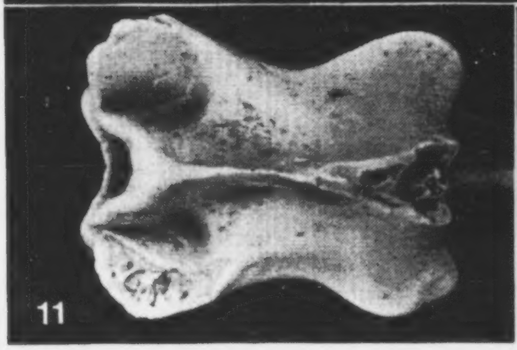
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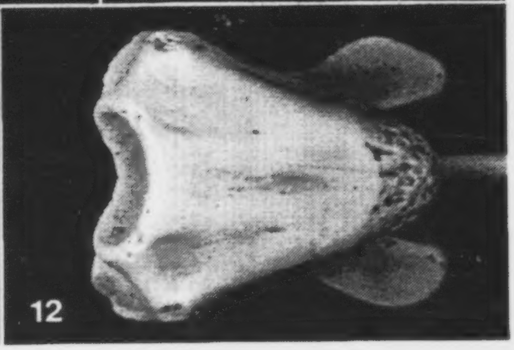
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Plate 15

Necrosauridae, Parasaniwa n. sp. (cf. P. wyomingensis), Oldman Formation, Alberta

Fig. 1. UALVP 33346, right maxillary, lateral view. About X 4

Fig. 2. UALVP 33346, medial view. About X 4

Fig. 3. RTMP 81.38.4, right maxillary, medial view. About X 4

Fig. 4. UALVP 33370, left dentary, medial view. About X 4

Fig. 5. UALVP 33371, right dentary, medial view. About X 4

Fig. 6. UALVP 33374, right frontal, dorsal view. About X 4

Fig. 7. UALVP 33374, ventral view. About X 4

Fig. 8. UALVP 33375, parietal, dorsal view. About X 4

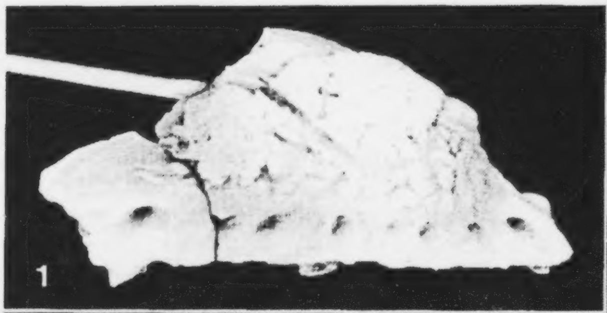
Fig. 9. UALVP 33375, ventral view. About X 4

?Parasaniwa sp., Milk River Formation, Alberta

Fig. 10. UALVP 33923, fragmentary left dentary, medial view. About X 6.5

Fig. 11. UALVP 33924, fragmentary left maxillary, medial view. About X 6.5

Fig. 12. UALVP 33925, fragmentary right dentary, medial view. About X 6.5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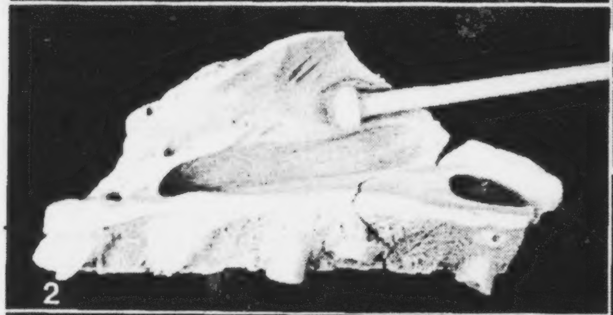
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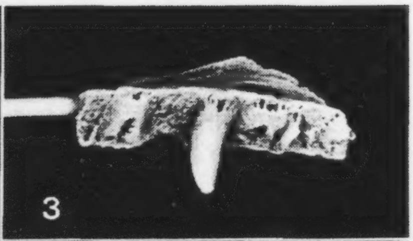
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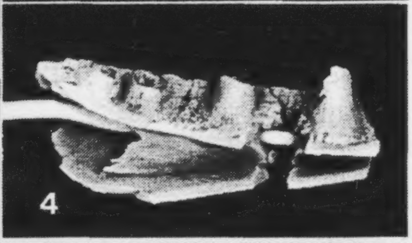
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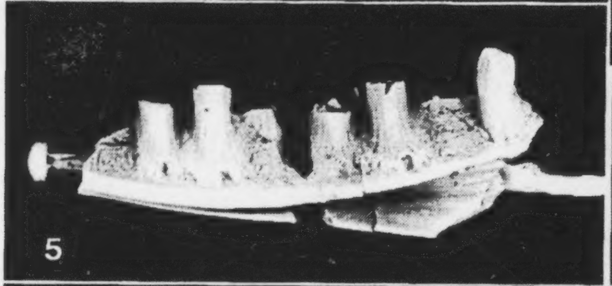
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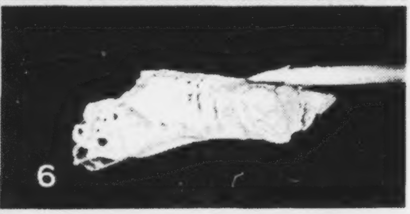
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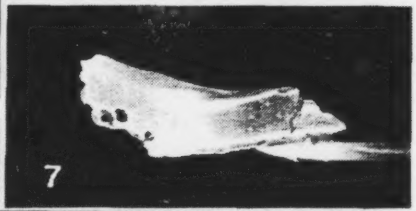
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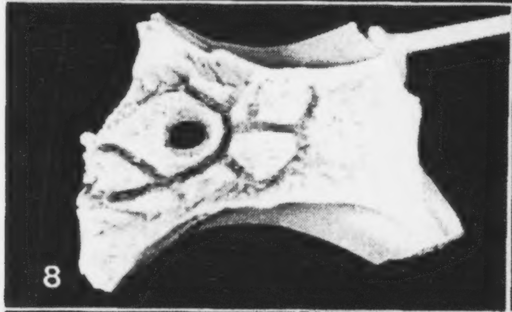
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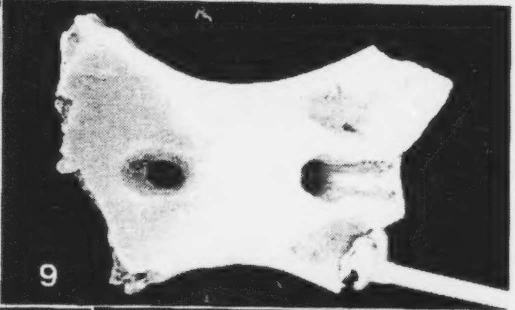
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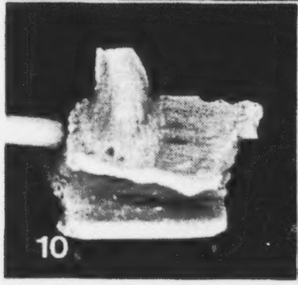
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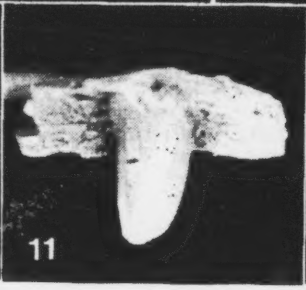
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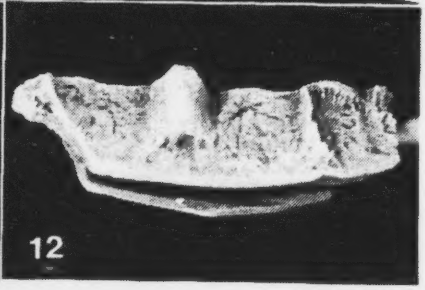
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Plate 16

Helodermatidae, Paraderma bogerti, Lance Formation, Wyoming

Fig. 1. UCMP 54261 (holotype), left maxillary, lateral view. About X 2

Fig. 2. UCMP 54261, medial view. About X 2

Fig. 3. UCMP 54261, dorsal view. About X 2

Paraderma bogerti, Scollard Formation, Alberta

Fig. 4. UALVP 29845, nearly complete left dentary, lateral view. About X 2

Fig. 5. UALVP 29845, medial view. About X 2

Fig. 6. UALVP 33385, incomplete parietal, dorsal view. About X 2

Fig. 7. UALVP 33385, ventral view. About X 2

Fig. 8. UALVP 33902, cervical vertebra, lateral view. About X 2

Fig. 9. UALVP 33903, dorsal vertebra, anterior view. About X 2

Fig. 10. UALVP 33903, lateral view. About X 2

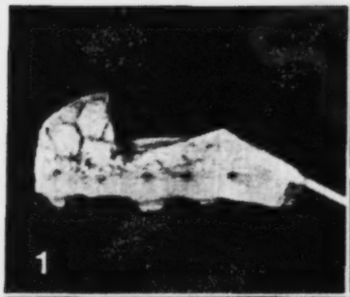
Fig. 11. UALVP 33903, ventral view. About X 2

Paraderma bogerti, Frenchman Formation, Saskatchewan

Fig. 12. UALVP 29846, fragmentary right dentary, medial view. About X 2

Fig. 13. UALVP 33387, dorsal vertebra, dorsal view. About X 2

Fig. 14. UALVP 33387, lateral view. About X 2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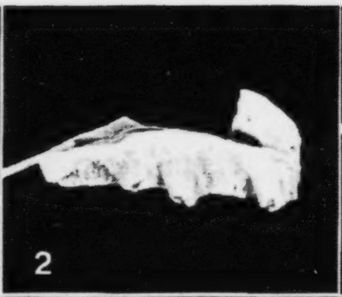
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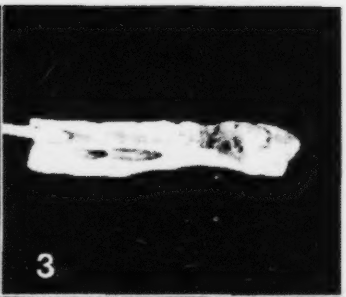
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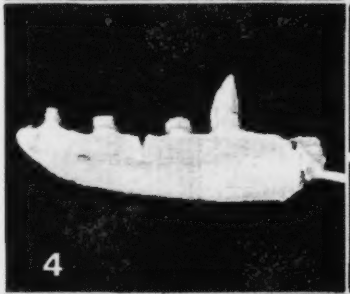
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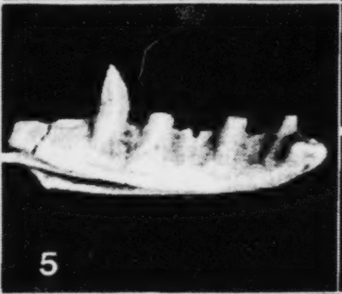
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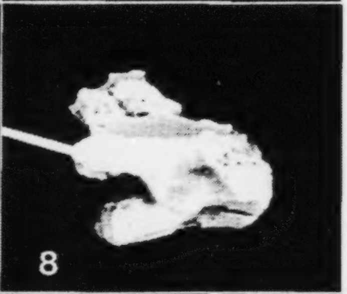
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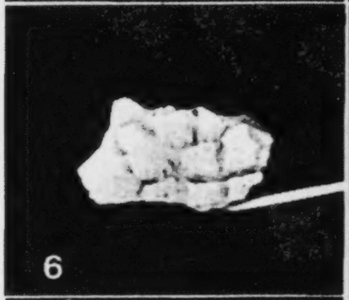
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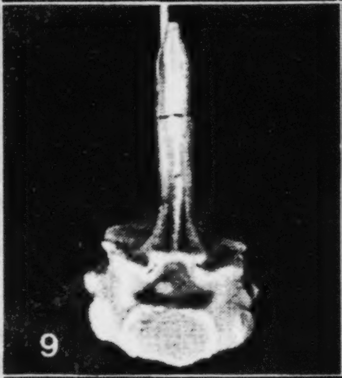
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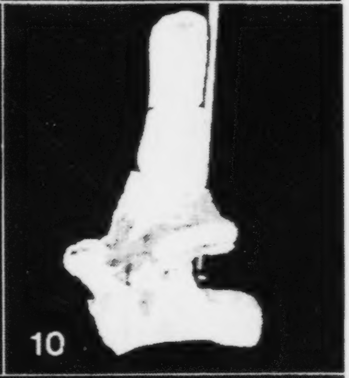
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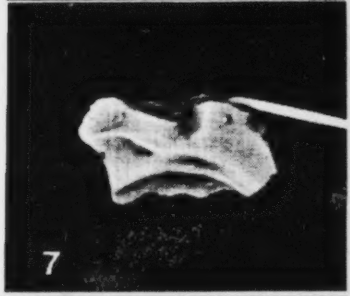
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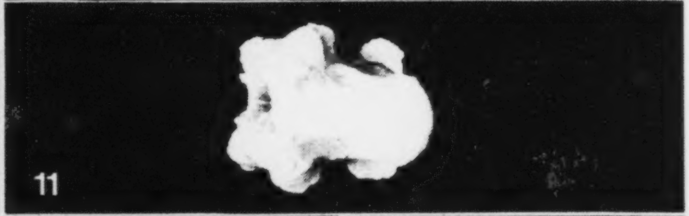
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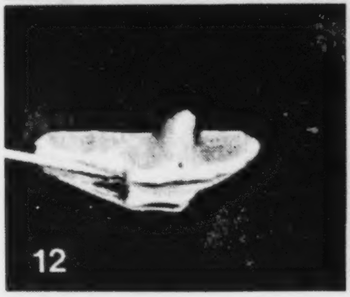
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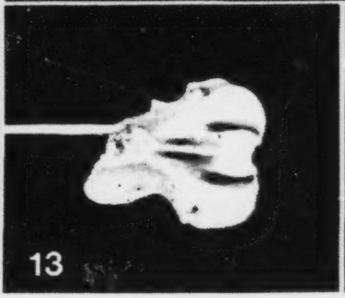
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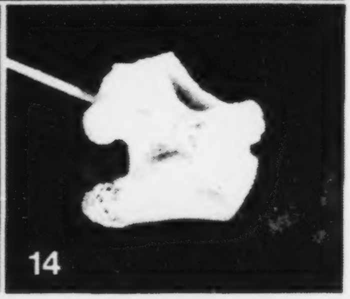
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Plate 17

Helodermatidae, Labrodioctes montanensis n. gen. et sp., Judith River and Oldman formations, Montana and Alberta

Fig. 1. ANSP 18664 (holotype), left dentary, lateral view. About X 1.6

Fig. 2. ANSP 18664, medial view. About X 1.6

Fig. 3. RTMP 78.18.1, incomplete left frontal, dorsal view. About X 2

Fig. 4. RTMP 78.18.1, ventral view. About X 2

Fig. 5. RTMP 78.18.1, lateral view. About X 2

Helodermatidae, genus & species undetermined, Oldman Formation, Alberta

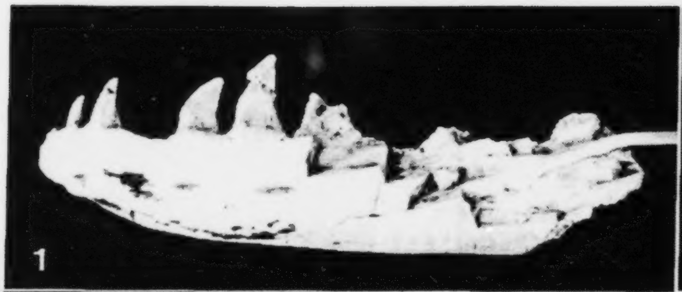
Fig. 6. RTMP 85.58.58, incomplete parietal, dorsal view. About X 2

Fig. 7. RTMP 85.58.58, ventral view. About X 2

Fig. 8. RTMP 88.36.212, incomplete frontals, dorsal view. About X 2

Fig. 9. RTMP 88.36.212, ventral view. About X 2

Fig. 10. UALVP 33338, tooth-bearing pterygoid, ventral view. About X 2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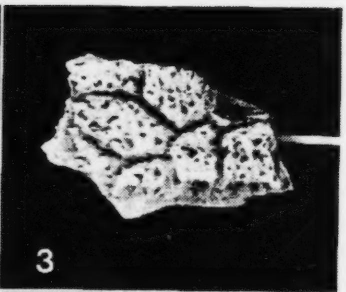
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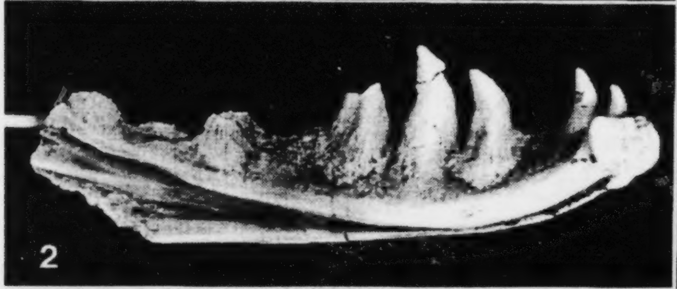
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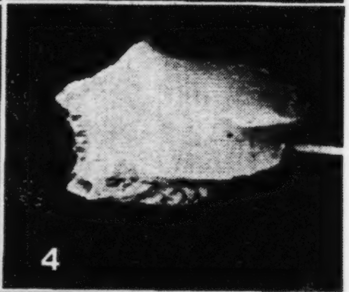
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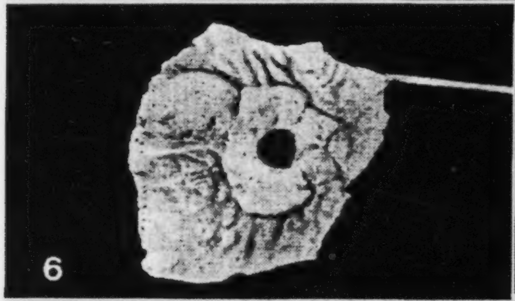
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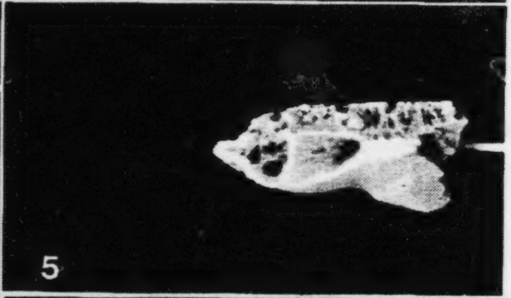
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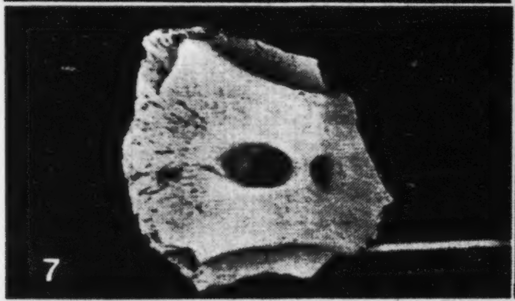
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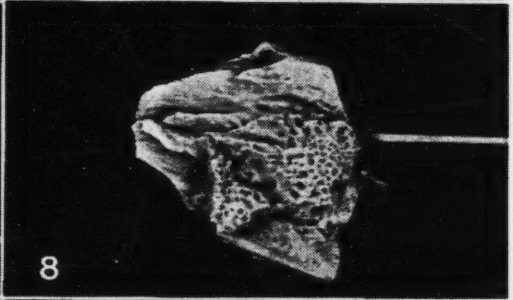
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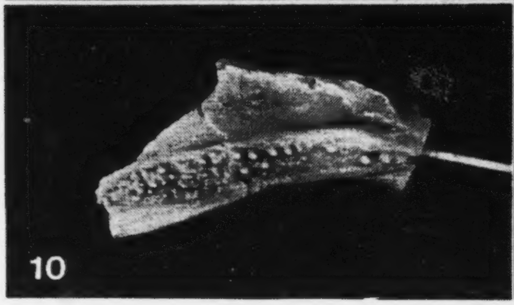
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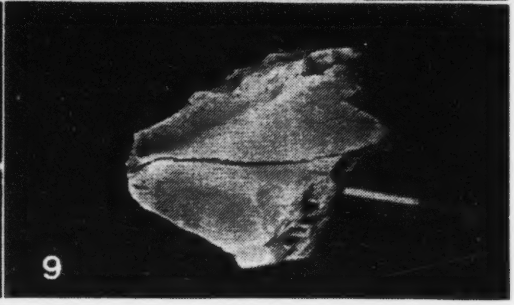
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Plate 18

Varanidae, Palaeosaniwa canadensis, Oldman Formation, Alberta

Fig. 1. RTMP 80.29.120, left maxillary, lateral view. About X 2

Fig. 2. RTMP 80.29.120, medial view. About X 2

Fig. 3. RTMP 80.20.37, right maxillary, lateral view. About X 2

Fig. 4. RTMP 80.20.37, medial view. About X 2

Fig. 5. RTMP 89.36.101, incomplete left dentary, medial view. About X 2

Fig. 6. RTMP 89.121.1, incomplete right dentary, lateral view. About X 2

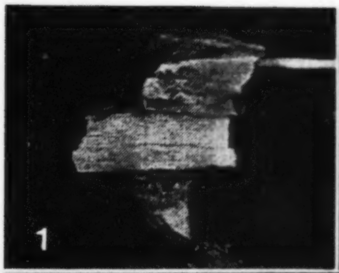
Fig. 7. RTMP 89.121.1, medial view. About X 2

Fig. 8. RTMP 85.36.184, incomplete right dentary, medial view. About X 2

Fig. 9. UALVP 33342, dorsal vertebra, lateral view. About X 2

Fig. 10. UALVP 33342, ventral view. About X 2

Fig. 11. UALVP 33344, dorsal vertebra, dorsal view. About X 2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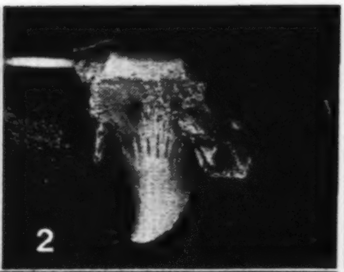
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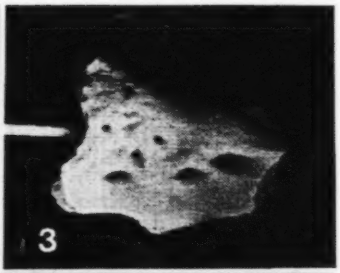
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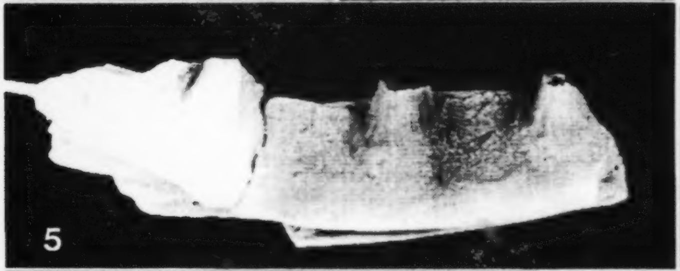
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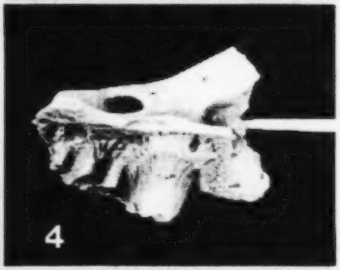
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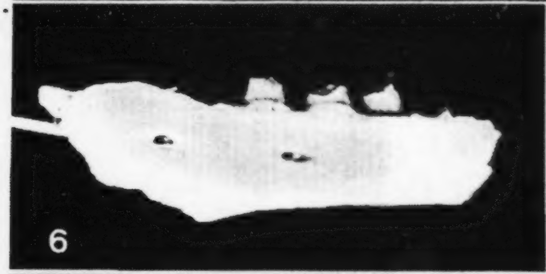
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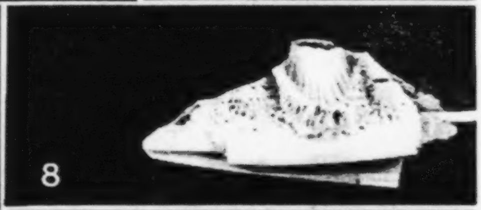
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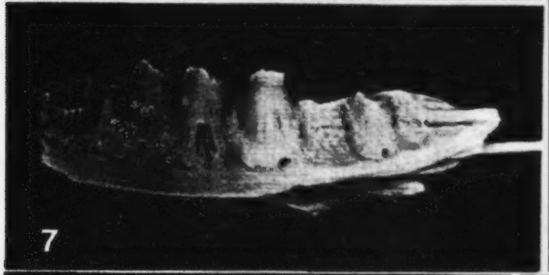
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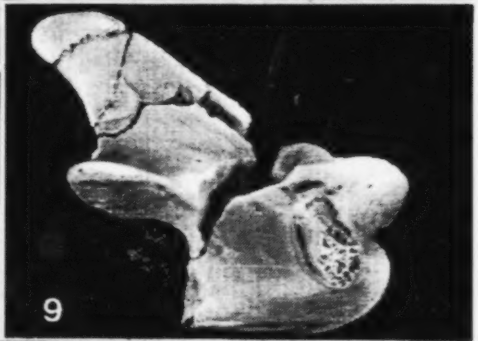
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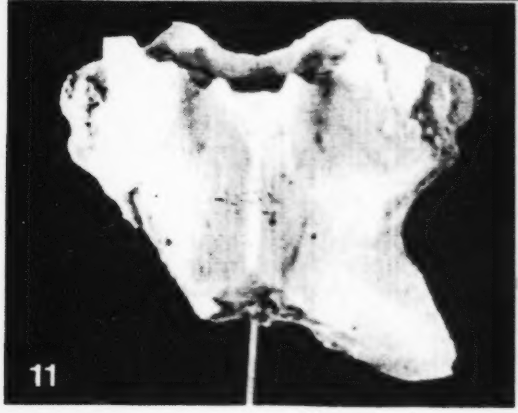
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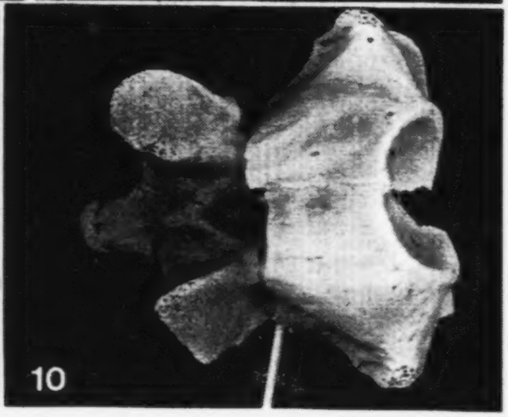
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